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Modelling walrus population dynamics: A direction for future assessments

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Walruses are harvested for subsistence in northern Canada. In this study a surplus production model was fitted to aerial survey data of abundance using Bayesian methods. The model was fitted to abundance data from two stocks: the Hudson Bay-Davis Strait stock and the Foxe Basin stock. The model estimated that walrus abundance in the northern Hudson Bay region of the Hudson Bay-Davis Strait stock declined from approximately 10,400 animals (rounded to the nearest 100) in 1954 to a minimum of 3,900 animals in 1986, but has increased since then to 7,000 walruses (95% Credibility Intervals =4,100–10,800). The model estimated a current population abundance in Foxe Basin of 12,500 (95% Credibility Intervals 8,600–18,500, rounded to the nearest 100). This population appears to have remained stable over the last 60 years. Walrus are considered Data Poor, consequently, Total Allowable Removals have been estimated using the Potential Biological Removal method. The population model can be used to provide inputs needed to estimate allowable removals. Given more data, the population model can be used to evaluate the probability that different harvest scenarios will meet management objectives.

Modélisation de la dynamique de population de morse : une voie pour les évaluations futures.

RÉSUMÉ

Les morses font l'objet d'une chasse de subsistance dans le nord du Canada. Dans la présente étude, un modèle de production excédentaire a été ajusté aux données du relevé aérien de l'abondance au moyen de méthodes bayésiennes. Le modèle a été ajusté en fonction des données sur l'abondance de deux stocks : le stock du détroit de Davis et de la baie d'Hudson, et le stock du bassin Foxe. Selon le modèle, on a estimé que l'abondance de morses du stock du détroit de Davis et de la baie d'Hudson dans la région du nord de la baie d'Hudson avait diminué, passant d'environ 10 400 animaux (arrondi à la centaine près) en 1954 à un minimum de 3 900 animaux en 1986, mais avait augmenté depuis pour remonter à 7 000 morses (intervalles de crédibilité de 95 % = 4 100 - 10 800). Le modèle a aussi permis d'estimer que l'abondance de la population actuelle dans le bassin de Foxe était de 12 500 animaux (intervalles de crédibilité de 95 %= 8 600 - 18 500 animaux, arrondis à la centaine près). La population semble être demeurée stable au cours des 60 dernières années. Le morse est considéré comme étant une espèce avec peu de données, en conséquence, le total autorisé des captures a été estimé à l'aide de la méthode du retrait biologique potentiel. Le modèle de population peut fournir les données nécessaires pour estimer les prélèvements autorisés. Avec plus de données, le modèle de population pourrait servir à évaluer la probabilité que divers scénarios de prélèvement atteignent les objectifs de gestion.

INTRODUCTION

The primary goal of a management model is to use data to make decisions that result in meeting management objectives that are usually defined by law, regulation or some management body (Taylor et al. 2000). The management of marine mammals in Canada is governed by the *Fisheries Act*, *Oceans Act* and *Species at Risk Act*. None of these pieces of legislation specify management objectives, consequently marine mammal harvesting in Canada is managed using a patchwork of approaches such as sustainable yield (Nunavik beluga, Doniol-Valcroze et al. 2013), a Precautionary Approach framework with precautionary and reference limit levels (Atlantic seal management, e.g., Hammill and Stenson 2007) and with harvests set using the Potential Biological Removal (PBR) formula (e.g., narwhal, bowhead, walrus, Doniol-Valcroze et al. 2015a, b, Stewart and Hamilton 2013).

PBR has found wide application in Canada in recent years because it requires only a single estimate of abundance (and standard error) to generate an allowable harvest that has a very low probability of causing significant harm to the stock. Unfortunately, in Canada, abundance data are limited for many marine mammal stocks (e.g., walrus), so PBR has fulfilled a need to provide harvest advice in such data-poor situations. However, the PBR was developed in tandem with the *Marine Mammal Protection Act* (MMPA) in the United States, which identified specific management objectives for this group of animals. In the United States, outside of Alaska, there is no directed harvesting of marine mammals. At the same time, it was realized that anthropogenic mortality of marine mammals would never fall to zero (e.g., incidental catches in fisheries). Therefore, some means was needed to identify an acceptable level of mortality that would allow industrial activities (e.g., fishing) to continue and would still fulfill the management objectives of the MMPA. The main management objective of the MMPA is to allow a stock to reach or maintain its 'Optimum Sustainable Population', which is defined as a population level between carrying capacity and the population level at maximum net productivity MNPL (Wade 1998), which can also be considered the population size that provides Maximum Sustainable Yield. An underlying philosophy behind PBR is that it does not address whether a population is increasing or not, or where it is situated with respect to MNPL. Instead, it addresses whether the level of removals could lead to a decline below MNPL (see Wade 1998 and references therein; Taylor et al. 2007). Simulation trials have shown that the method performs well with respect to the management objective under different types of bias and uncertainty (Wade 1998).

PBR is easy to estimate (see Wade 1998; Hammill et al. 2016a, b). Owing to its conservative properties, PBR can perform very well when there is considerable uncertainty associated with our understanding of the resource (Milner-Gulland et al. 2001; Wade 1998). There has been some debate on the strengths and weaknesses of PBR (e.g., Cooke et al. 2012; Lonergan 2011, 2012). The fact that PBR only requires a single population estimate (and standard error) is both a strength and a weakness. If only a single estimate is available, some advice on removals can be provided, but as more abundance information is accumulated, PBR levels will fluctuate with each new population estimate, often in ways that are not realistic for K-adapted species such as marine mammals, which adds to the difficulties for harvesters to plan harvesting activity and discourages buy-in into the management process. Moreover, PBR does not benefit from the information added by multiple survey estimates, meaning that additional data do not decrease uncertainty. Another problem is that the MMPA was designed to reduce takes to as close to zero as possible, therefore the PBR simulations did not consider the potential costs to harvesters of forgoing potential harvest. i.e., it only provides an estimate of removals that should allow a population to move towards or remain above MNPL. However, managers and harvesters are likely to make very different decisions concerning removals or takes that accept different levels of risk for populations that are abundant (e.g., harp seals> 7

million animals) compared to populations that are less abundant (e.g., St. Lawrence beluga <1200 individuals).

Surveys for marine mammals are often highly variable, insufficient to estimate vital rates and to understand mechanisms underlying population growth and decline. However, state-space models are a means of integrating data with population dynamics models and readily quantifying the various types of uncertainty, particularly when applied in a Bayesian framework. A state-space model consists of two components, a state process model and an observation model. The process model specifies the underlying dynamics of the population with the relevant population processes, such as the rate of increase, the density-dependent process, and carrying capacity (K), while the observation model relates the true population size to our observed information on abundance (Buckland et al. 2007; Mosnier et al. 2015; Wade 2000). This approach allows the simultaneous estimation of demographic parameters and the predicted trend of the population under different levels of harvest (Schaub and Abadi 2011; Mosnier et al. 2015; Doniol-Valcroze et al. 2013).

Abundance information for walrus populations in Canada is limited. However, time-series of counts are available for two of the four stocks of Atlantic walrus occurring in the central Arctic population (Fig. 1): nine surveys of walrus have been completed over the last 61 years in the Hudson Bay-Hudson Strait area and five surveys over the last 32 years in Foxe Basin. These surveys have differed in their methods, in area covered, and are characterized by large uncertainty. Bayesian statistics are well adapted to this situation because they allow the incorporation of prior existing knowledge of parameter values, including their associated uncertainty (Mosnier et al. 2015). In this paper, we have adapted a Bayesian model, that was initially developed for Eastern Hudson Bay beluga (Doniol-Valcroze et al. 2013), and applied it provide harvest advice for two stocks of Atlantic walrus in Canada. We have fitted the model to the Hudson Strait component of the Hudson Bay-Davis Strait and Foxe Basin stocks and used it to provide insights into the dynamics of each stock and provide recommendations for Total Allowable Removals. Since management objectives of walrus have not been stated clearly, we present the advice using two different management objectives: sustainable yield and PBR. Sustainable yield is the level of harvest that will allow the population to remain constant over a defined period of time. In this study, we define sustainable yield as harvest levels projected over a 10-year period that do not result in a decline of the population below 2014 levels. The objectives of PBR have been outlined in detail above, but here we estimate the PBR levels using outputs from the population model in order to benefit from all the available information rather than a single abundance estimate. We also discuss some of the implications of using these two approaches.

MATERIALS AND METHODS

SURVEYS

Hudson Bay-Davis Strait (HBDS) stock

A total of nine surveys have been flown to obtain estimates of abundance in the Hudson Bay-Hudson Strait area of this stock (Table 1). In August 1952, preliminary aerial surveys were flown at low altitude over Nottingham, Salisbury, Walrus and White islands using a RCAF Lancaster bomber, but no walrus were observed (Loughrey 1959). In July 1953, a flight with the US Fish and Wildlife Service over Coats and Walrus islands only detected 30 animals, but it was noted that animals began to scramble for the water when the aircraft was more than a ¼ mile away. The aircraft type was not specified. Further testing suggested that survey altitudes of 305 to 457 m minimized disturbance and in August 1954, two surveys were completed over seven haulout

sites around Southampton-Walrus-Coats islands using a twin engine Anson 1954 (Loughrey 1959). This resulted in an average count of 2,900 animals, which the author felt to be within 15% of accuracy. We interpreted this as a coefficient of variation of 15%. A combination of boat and aerial surveys of the same area resulted in a count of 2,650 animals in 1961 (Mansfield 1962). Twelve flights in July–August 1976, and 10 flights were made in July and August 1977 around the Southampton-Walrus-Coast Island area flying at an altitude of 150 to 250 m. The surveys involved a combination of visual and photographic observations (Mansfield and St. Aubin 1991). We took the average of all 1976 flights to obtain a mean estimate for 1976. In 1977, only 26 animals were observed on one flight and six on a second flight. These counts were not included, leaving eight counts which were used to obtain a mean estimate for 1977 (range 139–2171) (Mansfield and St. Aubin 1991, Hammill et al. 2016a)(Table 1). Coastal surveys were completed around the same area, and included Nottingham and Salisbury islands as well during July–August in 1988, 1989 and 1990. Line transect surveys were flown using Twin Otter flying at 150 m in Hudson Strait from the eastern entrance of the Strait to as far west as about the northwestern point of Mansell Island during March–April 2012 (Elliot et al. 2013). Finally, a coastal survey covering Hudson Strait, Southampton, Walrus, Coats and Mansell islands was flown in September 2014. The survey altitude was 204–305 m. Visual and photographic data were collected (Hammill et al. 2016a). Since the Southampton/Coats Island and Nottingham/Salisbury Island complexes appear to account for the majority of walrus observations, these were considered as relatively complete surveys for looking at the northern Hudson Bay-Hudson Strait component of this stock.

The aerial surveys, with the exception of the March–April 2012 survey (Elliot et al. 2013) only report counts of animals hauled out. These counts must be corrected for the proportion of animals that are hauled out during the survey. Telemetry data are not available for these surveys, therefore we used a mean haulout proportion of 0.3 (SE=0.18) which was estimated from several published studies (Table 1 in Hammill et al. 2015). The line-transect survey of Hudson Strait already included corrections for perception and availability bias (Elliot et al. 2013).

Foxe Basin stock

A total of five different survey studies were completed to obtain information on walrus abundance in Foxe Basin (Table 2). The Foxe Basin abundance estimates were based on haulout counts from surveys flown in July–September 1983, 2010 and 2011, and systematic strip-transect surveys flown in July–August 1988 and 1989 (Orr et al 1988, Richard unpublished report, Stewart and Hamilton 2013, Stewart and Higdon unpublished report). As these data represent counts of animals hauled out, they need to be adjusted by the proportion of the population hauled out when the survey was flown.

On 19 and 20 August 1983, flights were flown, at an altitude of 61–457 m, with 150 m being the preferred altitude. A total of 2,722 walrus were counted (Orr et al. 1988).

During August 1988 and July 1989, east-west systematic strip transects were flown using a DeHavilland Twin Otter flying at an altitude of 457 m. Four hundred and forty-three walrus were counted in 1988, and 476 walrus were counted in 1989 (Higdon and Stewart unpublished report, Hammill et al. 2016b). This resulted in a hauled-out count of 5,126 (SE=4,390) in 1988 and 5,510 (SE=1,644) in 1989.

During August and September of 2010 and 2011 surveys were also flown in Foxe Basin using a de Havilland Canada DHC-6 Twin Otter at a target altitude of 300 m ASL and speed of 210 km/h flying approximately 1 km off the coastline (Stewart et al. 2013). Both visual and photographic data were collected. A time-distance criterion (45 km/24 h) was applied to reduce the probability of double-counting walrus at different haulouts, which meant that final counts were based on fewer haulout sites than were examined in total (Stewart et al. 2013). A total of

3,661 walrus were counted in 2010. Two haulout counts in 2011 resulted in 5,946 and 4,484 animals. Taking the average for the two, resulted in an average haulout counts of 5,214 (SE=1,333) walruses.

The Foxe Basin counts were not adjusted for animals in the water at the time the studies were completed. Satellite transmitters were deployed on animals in Foxe Basin during the 2010 and 2011 surveys and these were used to adjust the haulout counts of all surveys using a mean proportion of animals hauled out of 0.37 (SE=0.16) (Table 2).

HARVEST RECORDS

Harvest data are available from annual reports of landed catches (Table 3.4)summarized in Hammill et al. 2016a, b). We assume that all walruses harvested by the communities in Hudson Strait, Ungava Bay, western Hudson Bay (Arviat, Chesterfield Inlet, Coral Harbour, Rankin Inlet, Naujaat (Whale Cove), eastern Hudson Bay (Akulivik, Puvirnituq) and the east Baffin Island communities of Iqaluit, Pangnirtung, Qikiqtarjuaq, and Clyde River are from the HBDB stock. We did not include harvests from Greenland. Similarly, it was assumed that animals harvested from the Foxe Basin stock were taken only by hunters from the communities of Igloolik and Hall Beach. The harvest records had several years where data were not reported. We substituted the average harvest of the most recent five years for the missing data (Tables 3, 4). Similarly, not all walrus that are killed are recovered and reported. Information on loss rates is limited. Loss rates of 20–30% have been reported for Greenland (Witting and Born 2005), and 30-40% for harvesting in Canada (Loughrey 1959). More recent estimates from the 1970s and 1980s range from 30–38% (Mansfield 1973, Orr et al. 1988, Freeman 1974/75 in Stewart et al. 2014). NAMMCO assumes a Struck and Loss of 30% unless there is more specific information available (DFO 2002, NAMMCO 2006). We incorporated this range of estimates in the prior formulation for the struck and loss factor (see below).

MODEL SPECIFICATION

A stochastic stock-production model, assuming density dependence acting on the population growth rate, was fitted by Bayesian methods. We sought to separate the observation error (associated with data collection and abundance estimation) from the process error (arising from natural variability in population dynamics). To this end, we developed a hierarchical state-space model that considers survey data to be the outcome of two distinct stochastic processes: a state process and an observation process (de Valpine and Hastings 2002).

The state process describes the underlying population dynamics and the evolution of the true stock size over time, using a discrete theta-logistic model, i.e., a re-parameterization of the Pella-Tomlinson model (Pella and Tomlinson 1969, Innes and Stewart 2002). Population size in each year N_t (from 1954 to 2014) is a multiple of the previous year's, with removals deducted:

$$N_t = N_{t-1} + N_{t-1} \cdot (\lambda_{max} - 1) \cdot \left[1 - (N_{t-1}/K)^{\theta}\right] \cdot \varepsilon_{p_t} - R_t \text{ , with } \varepsilon_{p_t} \sim \log N\left(0, \tau_p^2\right)$$

where r_{max} is the maximum growth rate, K is environmental carrying capacity and theta θ defines the shape of the density-dependent function. ε_{p_t} a stochastic term for the process error and R_t are the removals for that year. Removals were calculated as reported catches, C_t, corrected for the proportion of animals that were struck and lost, SL:

$$R_t = C_t \cdot (1 + SL)$$

The observation process describes the relationship between true population size and observed data. In our model, survey estimates $\hat{N}_t$ are linked to population size N_t by a multiplicative error term ε_{o_t}:

$\delta_t = \theta_t \cdot \varepsilon_{t,y}$, with $\varepsilon_{t,y} \sim \log N(0, \sigma_y)$

PRIORS

Existing information, traditional knowledge, and expert opinion were used to formulate prior distributions for the random variables included in the model (Table 1). We did not know what the starting population might be, but provided a wide range that encompassed the adjusted estimate of walrus from surveys completed in 1990 by Loughlin (1994). The initial population size (N_{init}) was given a uniform prior between 100 and 30,000 individuals. In addition, we limited the initial population size, so that it could never be higher than K.

In previous assessments, the maximum annual rate of increase of walrus was set at $r_{max} = 0.07$ e.g., Stewart and Hamilton (2010), which agrees with some early work that estimated r_{max}. by fitting an exponential curve to Soviet estimates of abundance from 1958 to 1975, when walrus were not considered to be food-limited (Sease and Chapman 1988). However, this estimate is likely to be conservative because it did not take into account the impacts of harvesting on population growth. More recent modeling suggests that the maximum rate of increase is 11% (Chivers 1996, Taylor and Udevitz 2015, Atkins and Born 2016) and this is the default used in the United States in the most recent assessments of Pacific walrus. Consequently, in this assessment a r_{max} of .09 was used.

We know little about carrying capacity and the likely density dependence parameter for walrus in the Hudson Strait area of the Hudson Strait-Davis Strait stock. For K, we used a uniform prior of 500 to 35,000, which encompassed the starting population size. Marine mammals are considered to reach maximum productivity between 50 and 60% of K (Taylor and Gerrodette 1993), which results in theta lying roughly between 1 and 7. Trujillo et al. (2006) used theta =2.4 to model the dynamics of gray seals (*Halichoerus grypus*), while recent work on walrus has used a range of values from 1 to 4 (Chivers 1996). Atkins and Born (2016) modeled the dynamics of Greenland walrus populations and allowed the model to estimate theta. Their posterior values for theta were generally around 2.7 (95% credibility intervals 1.1–7.3). We assumed a uniform distribution for theta with a range of 1 to 7 (Table 1).

Reported harvests underestimate the number of walrus killed because of animals wounded or killed but not recovered, as well as an absence of harvest reports for some communities in different years. For communities with missing report data, we estimated the average number of walrus reported killed based on the most recent 5 years with harvest data. The total walrus in walrus hunts are not known exactly. We gave the struck and lost correction factor (b_t) a moderately informative prior following a Beta (3, 4) distribution, with a median of 0.42 and quantile points at 0.29 and 0.58.

The stochastic process error terms ($\varepsilon_{t,y}$) were given a log-normal distribution with a zero location parameter. The precision parameter for the lognormal distribution was assigned a moderately informative prior following a gamma (1.5, 0.031) distribution. These parameters were chosen so that the resulting error multiplier would have a median of 1 and quantiles of 0.85 and 1.15 reflecting our belief that walrus stock dynamics are not highly variable.

The uncertainty associated with each survey is poorly estimated. Therefore, the uncertainty was incorporated into the fitting process only by guiding the formulation of the prior distribution of the survey error. The survey error term (ω_y) followed a log-normal distribution with a zero location parameter. Its precision parameter was given a moderately informative prior following a gamma (2.5, 0.4) distribution. These parameters were chosen so that the resulting CV on the survey estimates would have quantiles of 20% and 95%, which are approximately equivalent to the range of what we consider to be plausible CV for the survey abundance estimates.

[illegible]

[illegible]

[illegible]

95% CI=4.804–17.861). The theta prior introduced into the Foxe Basin model was based on the updated theta posterior from the HBDS model. We used a prior of (0.6+7*beta(2,3)). This prior had a mean of 3.4 (95% CI=1.1–6.3) compared to the Hudson Bay-Davis Strait posterior with mean of 3.3 (1.1–6.7). The prior was not updated (Table 6b, Fig. 4b). The prior for struck and lost introduced into the Foxe Basin model was also based on the updated struck and loss posterior from the HBDS model. Instead of using a beta distribution of beta (3,4), with a mean of 0.43 for the prior, we used a beta (2,4), with a mean of 0.35. This resulted in only minor changes for the Foxe Basin stock struck and lost parameter to a posterior mean of 0.33 (Table 7, Fig. 11).

In the Foxe Basin model, all five survey point estimates are either just on, or lie within the 95% credibility intervals (Fig. 12). The model estimated a mean starting 1954 population (before harvesting) of 11,982 (median=12,205, 95% CI=4,804–17,861)(Table 7). The model indicates that there has been little change in the population over the last 60+ years. The mean 2014 estimated (after harvesting) population is 12,489 (Median=12,158, 95% CI=8,574–18,493) (Fig. 12). The estimated theta had a median value of 3.4, which means that maximum productivity of the stock would occur at 65% of carrying capacity.

Sustainable yields are defined as harvests that result in less than a 50% probability of decline. The probability that reported harvests of 190, 183 and 172 animals from the Foxe Basin stock over the next 10 years would result in a population decline below 2014 levels was 10%, 50% and 80% respectively (Fig. 13, 14). The PBR estimate for the stock using the model estimate of population size in 2014 is 422, assuming a Recovery Factor of 1. This estimate is higher than the estimate of 385 from Hammill et al. (2016b). This figure does not take into account struck and lost. The mean struck and lost factor from the model was 0.33 (95% CI=0.05–0.71). Adjusting PBR to take into account struck and lost results in PBR estimates of 280 (95% CI= 122 to 400).

Reported harvests since 1954 in the villages of Igloolik and Hall Beach have been relatively stable, averaging 173 (SE=25) animals over the last five years (Fig. 10). At current harvest levels the model suggests that the population will decline below 2014 levels, but removals are below PBR levels after taking into account struck and lost in the PBR calculation.

DISCUSSION

Walruses are harvested for subsistence purposes throughout much of their range in Canada, Greenland and Alaska. Moreover, in some areas there is a small sports harvest. Once widely distributed in the eastern Canadian Arctic, Hudson and James bays, and down the Atlantic coast, to the Gulf of St Lawrence and Sable Island (e.g., Stewart et al. 2014), their current distribution appears to be restricted to northern Hudson Bay, and northwards, with only a few now seen south of Labrador and James Bay (Born et al. 1995, Stewart et al. 2014, Clark undated, in Loughrey 1959, COSEWIC 2006). Their gregarious nature makes walruses vulnerable to large local takes and, coupled with a narrow trophic niche and restricted seasonal distribution, makes them vulnerable to environmental changes (Born et al. 1995, COSEWIC 2006, Stewart et al. 2014).

Unfortunately, survey activity of the individual stocks, and demographic information on walrus in Canada are limited. There have been some abundance surveys flown in Foxe Basin and northern Hudson Bay/Hudson Strait, which forms part of the HBDS stocks, but in the case of the latter stock, some of these surveys date back over 50 years and they appear to have covered only the major haulout sites.

State-space models particularly when applied in a Bayesian framework, are a means of integrating data with population dynamics models and readily quantifying the various types of

uncertainty (Buckland et al. 2007), which makes this approach suited for application to walrus, where the data are limited and very uncertain. Using Bayesian methods, we fitted a surplus production model to these highly uncertain data, taking into account harvest information that extended back to the early 1950s, to obtain estimates of abundance, population trend and to identify the impact of future harvests on the population. Additional uncertainty is associated with several of the model parameters including, the estimated rate of increase of the stock, the correction factor for diving animals, estimates of struck-and-loss, and environmental carrying capacity. However, Bayesian methods allowed us to explicitly incorporate uncertainty around these parameters (Wade 2000), which are represented in the model by statistical distributions instead of single values. Bayesian fitting also ensured that uncertainty was propagated throughout the analysis, and that the correlations among parameters were preserved (Hoyle and Maunder 2004). The resulting stock trajectory is based on realistic population dynamics and offers more information than a simple trend analysis. It also allows for the explicit expression of the risk associated with different levels of harvest within the context of whether these harvests will respect management objectives.

We made certain assumptions about the prior distributions of the model parameters. Sensitivity analyses showed that these assumptions have a small impact on the final estimates of abundance, but can have a strong effect on the uncertainty around estimates, on future population trajectories, and on our interpretation of parameter values. For instance, point estimates of stock size were little influenced by changes in the hyper-parameter α as used in the prior distribution of the survey error. Their 95% CI, on the other hand, increased markedly with increasing values of α (which increase the CV of survey estimates). In other words, postulating higher uncertainty around aerial survey estimates also increased the uncertainty around model estimates. However, we note that the model was effective in reducing our uncertainty around our estimates of walrus abundance.

POPULATION MODELLING AND PARAMETER ESTIMATES

The estimated shape of the density-dependent parameter (θ) was well updated from its flat prior distribution in the HBDS model. The median value of 3.3 (HBDS model), was slightly higher than median values of 2.7 to 2.9 for walrus in Greenland, but were well within the 90% Credibility Intervals (Witting and Born 2005), resulting in Maximum Sustainable Yield levels at around 67% of K. On the other hand, theta values in the Foxe Basin model were not updated, indicating that there was insufficient information in the model to modify these values, which is not surprising, since the model shows a flat trajectory over the last 60 years. There is some discussion concerning the maximum annual growth rate of walrus populations (see Materials and Methods), but 1.08 has been used as a default. We fixed this parameter, but realized growth rates were determined by both the shape parameter (θ) and the model estimates of population abundance in relation to K, with the result that the effective growth rate was normally much lower than the default. The model provided estimates of K, but we are unable to say how realistic these estimates might be. Recent efforts to reconstruct catch histories (Stewart et al. 2014) for some stocks may provide an opportunity to reconstruct pre-exploitation estimates of the population, which, although they may not be the same as current K, would still provide insights into possible carrying capacity levels.

The numbers of animals struck and lost are an important input into the models. Several estimates of Struck and Lost have been reported in the literature (see above), but these have been determined from different harvests in different areas and different time periods. The struck-and-lost factor was introduced into the model assuming a beta distribution, with a prior value of 42.2% (95% CI 12–78%), that we have used for Nunavik beluga. This is not to say that struck and lost rates for beluga and walrus are the same, but the beluga example provided suitable information that could be introduced into the model as a prior. When modelled for the

HBDS walrus stock, the prior was updated from a mean of 42% to a mean of 35% (95% CI=23 to 45%), which is comparable to a quasi-default value of 0.3 used by NAMMCO (2006). This posterior was subsequently used as prior in the Foxe Basin walrus models, but showed little modification from its prior values. This could suggest that the struck and lost distributions are similar between the two areas, and between studies, which is possible, but could also be explained by the fewer survey points flown in the Foxe Basin within a more restricted period, and a flat population that does not bring enough information to update the struck and lost parameters. One final consideration is that although defined as the proportion of animals that are struck and not recovered, this factor also include the effects of under-reporting (of which struck-and-lost is a subset).

In the HBDS model, K was moderately correlated with the struck and lost parameter, negatively correlated with the initial population size and had a small correlation with the abundance estimate for 2014. In the Foxe Basin models, a strong correlation was only observed between the carrying capacity parameter (K) and the 2014 estimate of population size. Overall, these correlations indicate that the historical population has remained close to carrying capacity, or because of a lack of a strong change, our modelling approach cannot provide credible information as to the actual values of these parameters. However, any independent estimation of the value of one or more of these parameters from a dedicated field program would increase our confidence in the estimation of the others as well as the accuracy of future projections.

POPULATION TRAJECTORY AND HARVEST LEVELS UNDER THE PRECAUTIONARY APPROACH

The HBDS model Run 1 assumed that animals that were surveyed in Hudson Strait in March–April 2012, and during the surveys flown during July–September in other years were available to harvesters living in Nunavik communities north of Inukjuak, the northwestern and northeastern Hudson Bay communities, Coral Harbour, Nunavut communities in Hudson Strait, and along the east coast of Baffin island. Walrus counts and harvests from Greenland, with which this stock is shared were not included. There is some movement between areas, but the level of exchange is not well understood. The surveys of the northern Hudson Bay-Hudson Strait area resulted in a population estimate of 7,000 (95% CI 4,100–10,800, rounded to the nearest 100). A 2007 survey of the east Baffin component of the HBDS stock resulted in an estimate of 2,500 (95% CI=1,800–3,500) for that region. It is not possible at the current time to add the two estimates together because of the seven year difference in timing of the surveys and because of uncertainty in the extent of movement between Greenland, east Baffin Island and Hudson Strait. If the late summer-early autumn surveys of Hudson Strait-Hudson Bay represent the population harvested by hunters in this area, then perhaps modeling east Baffin and Greenland haulouts separately, as has been done to date is adequate (e.g., Witting and Born 2005, 2014).

Additional runs of the HBDS model excluded surveys flown prior to 1988. Excluding surveys from the 1970s, 60s and 50s essentially resulted in the model fitting to only two points, with a slightly higher estimate of the population in 2014 than was obtained using the more complete dataset. This also resulted in a higher estimate for PBR due to the higher estimate of population size as well as a slightly lower level of uncertainty associated with the population estimate. The earlier surveys did not cover as large an area as the surveys flown after 1988, but they did survey the main haulout sites and provided the model with useful information to improve fitting and updating of model priors such as K, theta, the starting population and struck and lost. Including these surveys indicated that the population was probably greater than it is today, and had probably declined after the 1950s, which is more in line with our understanding of the status of walrus in this area (e.g., see Loughrey 1959, Mansfield 1962).

The model did not fit well to the 1976 and 1977 data. Unlike the other surveys which were based on only one or two counts of important haulout sites, the July–August, 1976–1977 estimates were mean counts from multiple surveys carried out over a 2 month period in the Southampton-Coats Island area. These counts were highly variable (Mansfield and St. Aubin 1991), reflecting the considerable variability in walrus haulout behaviour which we likely have not captured very well in our analysis of walrus counts (Doniol-Valcroze et al. 2016). Nonetheless, they provide useful information to the model. The model shows that the HBDS stock declined from the 1950s, reaching a minimum in the early 1990s, and is likely to be increasing under current reported harvests, while the Foxe Basin model suggest that there has been little change in stock size over the last 60 years. The HBDS benefitted from having more estimates of abundance that stretched out over many years. The Foxe Basin model had difficulties in reconciling the starting population size and environmental carrying capacity and there was a strong correlation between K and the model estimate of the 2014 population size. This may be linked to the fact that the first aerial survey of Foxe Basin was flown in 1982, but we incorporated into the model, harvest data that extended back to 1954, which may have provided the model with too much flexibility prior to the onset of the survey time series. We will continue to explore possible factors that might be affecting this model, but with no strong trend in harvests over the last 60 years, no clear trend in abundance, limited survey effort that is more constrained in time (compared to the HBDS model), there may not be enough information to inform the Foxe Basin model further. Thus this model believes that the current population is near stock carrying capacity, with little change occurring over the last 60 years.

In signing the United Nations Agreement for the Implementation of the Provisions of the United Nations Convention on the Law of the Sea relating to the Conservation and Management of Straddling Fish Stocks and Highly Migratory Fish Stocks, Canada has committed to managing fisheries resources to maintain or restore stocks to levels capable of producing maximum sustainable yield and to apply the precautionary approach with stock specific reference points. A precautionary approach framework was developed and implemented for Atlantic seals in 2003 (e.g., Hammill and Stenson 2003, 2007, 2013), while departmental guidelines were developed in 2006 (DFO 2006), and some additional discussions on the precautionary approach in Canada and in other jurisdictions has occurred within the marine mammal peer review group (e.g., Hammill and Stenson 2013; Doniol-Valcroze et al. 2013, Stenson et al. 2012). The DFO guidelines suggest that a precautionary reference level be set at 80% of the population size at Maximum Sustainable Yield (MSY), and a critical reference limit be set at 40% of the population size at MSY, which divides the management space into three zones, a healthy, cautious and critical zone. Where a stock lies with respect to the precautionary and critical reference limits, determines in which zone it lies. Within northern communities, harvesting is also governed by the different land-claim agreements, which tend to reflect two objectives:

i) subsistence harvesting can only be limited if there is conservation concern;
ii) harvesting is governed by the Principles of Conservation, which includes:
    a. the maintenance of the natural balance of ecological systems;
    b. the protection of wildlife habitat; the maintenance of vital, healthy, wildlife populations capable of sustaining harvesting needs as defined, and
    c. the restoration and revitalization of depleted populations of wildlife and wildlife habitat.

In the absence of a Precautionary Approach framework for walruses, we used two approaches to illustrate the risk of different harvest levels not respecting the management objectives we identified. We specifically tested the risk of a range of harvest levels not respecting a management objective of sustainable yield, where sustainable yield was defined as the number of animals that can be removed, in this case over a ten-year period, without resulting in the

population declining below 2014 levels. In a second approach we assumed that the management objective was to maintain the population above the level that results in MSY. We estimated acceptable levels of removals using population model outputs as data inputs for the PBR formula and compared these with PBR estimates from the most recent survey (Hammill et al. 2016a, b) We also incorporated the Struck and Lost posterior mean into the PBR estimate to provide a range of PBR values. Looking at the Hudson Bay Davis Strait stock, both the sustainable yield and PBR methods indicated that current harvests are likely to respect both of the identified management objectives here. The PBR indicated that hunters could remove up to 190 animals after taking into account struck and lost. Unlike what is normally done, using model outputs to calculate the PBR means that, this calculation benefits from the information contained in the full survey series and catch records. The model estimate of PBR is higher than the PBR estimate from the aerial survey, which including struck and lost had a PBR of 126, for F_R of 1. The difference results from the lower CV associated with the population model estimate of the 2014 walrus population. For example the CV associated with the survey estimate of the population size is 0.58. The CV associated with the estimate of population size that is obtained from the population model is 0.23. In other words, the higher precision of the model estimate, which benefits from additional information compared to traditional PBR calculations, could result in a larger allowable harvest while still adhering to the same precautionary principles.

For the Foxe Basin stock, there were major differences in allowable harvests between the sustainable yield harvest estimates and those obtained from PBR. These differences arise from the underling differences in management objectives between the two approaches and where the two stocks lie with respect to estimated environmental carrying capacity. The Foxe Basin stock appears to be close to K. Owing to density-dependent factors affecting the dynamics of the stock, this means that the effective rate of increase of the population was less than 2%. To maintain a constant population, only about 2% of the resource was potentially available to harvesters if the management objective was that of sustainable yield. However, the management objective for PBR is to maintain a population above MSY. For walrus, PBR assumes that the rate of increase is fixed at ½ of the maximum rate of increase, which for walrus we defined as 4% (50% of 0.08), resulting in a PBR estimate of 290 animals. The comparable estimates of PBR from the aerial surveys with F_R=1 (i.e., after taking into account struck and lost) were 206 using the 2010 survey and 269 using the 2011 survey estimate. The difference is due to the lower CV in the 2014 estimate from the model (CV=0.20), than from the surveys alone (CV=0.43).

An alternative to PBR is to estimate removals directly using the population model and to provide an estimate of the probability or 'risk' that different harvest levels will respect the management objective. Assuming the PBR default that MSY occurs at 0.5K, then the model indicates that yearly harvests of 233 walruses from the HBDS stock would have a 95% probability of remaining above MSY after 10 years. Using the same approach to estimate harvests in Foxe Basin, then harvests of 418 would have a 95% probability of the population remaining above MSY, if MSY is set at 0.5 of K. Thus, one of the values of the population model approach is that the probability of respecting the management objectives can be presented and discussed in a more explicit manner than is possible using the PBR formula only.

In this study, a population model was fitted to very uncertain survey data, collected over the last 60 years, using Bayesian methods, to provide inference into the impacts of harvesting and insights into current abundance. The model has been developed to include the possibility that some communities may be harvesting from different stocks. However, for the simulations presented here, we assumed a single stock composition of the harvest in each model i.e., Igloolik and Hall Beach only harvested from the Foxe Basin stock, and communities in Ungava Bay, Hudson Strait, northeastern Nunavik, and northern Hudson Bay only harvested from the northern Hudson Bay component of the Hudson Bay-Hudson Strait stock, because the amount

of exchange between the different stocks is not known. As more information becomes available, this feature can easily be 'switched' on.

The model can also be used to provide a risk evaluation approach in evaluating whether different harvest or other removal scenarios (e.g., mortality due to ship strikes) will respect management objectives. Compared to the simplistic approach of PBR, the integrated population model improves our understanding of the dynamics of the population and helps to identify underlying uncertainties in the assessment that require additional work.

An important factor in any assessment is recent data on abundance. The HBDS stock was surveyed in 2014, but the Foxe Basin stock was last surveyed in 2011. Model uncertainty increases with increasing time since the last survey, which affects our ability to evaluate the impact of harvesting on the population. Thus new surveys will not only reduce current uncertainty, they will also, over time, reduce our reliance on the 'historical' surveys as new data are incorporated into the model.

In this study, we assumed that the proportion of animals hauled out was fixed and that the error around its estimate could be described using a binomial distribution. However, others have shown that haulout behaviour is more complex and variable than can be represented using a binomial distribution (Udevitz et al. 2009; Lydersen et al. 2008; Doniol-Valcroze et al. 2016). Trying to incorporate this uncertainty directly into the fitting process is one direction to try to improve the model. Struck and lost is an important source of uncertainty in marine mammal hunts. Improving information on struck and lost will not only improve model inference, related to this parameter, but may also reduce uncertainty in other model parameters as well. We did not examine the impacts of non-reporting. From the perspective of the model, non-reporting comprises an important subset of the struck and lost parameter, but in any harvest management, an understanding of actual removals is crucial. The impact of non-reporting is to increase uncertainty associated with struck and loss levels, which will result in more conservative estimates of acceptable take levels. Finally, we modelled Foxe Basin and HBDS walrus separately, assuming that they form two discrete stocks and that community harvests were assigned to the appropriate stock. Within the model, it is easy to include uncertainty related to stock identity of community harvests, but currently data are not available for this parameter.

LITERATURE CITED

Born, E.W., Gjertz, I. and Reeves, R.R. 1995. Population assessment of Atlantic walrus. Norsk Polarinst. Medd. 138: 100 p.

Brooks, S. P. and Gelman, A. 1998. Alternative methods for monitoring convergence of iterative simulations. J. Comput. Graph. Stat. 7:434–455.

Brooks, S., King, R. and Morgan, B. 2004. A Bayesian approach to combining animal abundance and demographic data. Anim. Biodivers. Conserv. 27: 515–529.

Buckland, S.T., Newman, K. B., Fernandez, C., Thomas, L. and Harwood, J. 2007. Embedding population dynamics models in inference. Statist. Sci. 22: 44–58.

Chivers, S.J. 1999. Biological indices for monitoring population status of walrus evaluated with an individual-based model. *In* Marine mammal survey and assessment methods. Edited by G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald, and D.G. Robertson. A.A. Balkema, Rotterdam, Holland. 287 p.

Cooke J., Leaper, R., Wade, P., Lavigne, D. and Taylor, B. 2012. Management rules for marine mammal populations: A response to Lonergan. Mar. Policy 36, 389–92.

COSEWIC. 2006. COSEWIC assessment and update status report on the Atlantic walrus *Odobenus Rosmarus rosmarus* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa, ix+65 pp.

de Valpine, P., and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. Ecol. Monogr. 72: 57–76.

DFO. 2002. Atlantic Walrus. DFO Sci. Stock Status Rep. E5-17, 18, 19, 20.

DFO. 2006. A Harvest Strategy Compliant with the Precautionary Approach. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2006/023

Doniol-Valcroze, T., Gosselin, J.-F., and Hammill, M.O. 2013. Population modeling and harvest advice under the precautionary approach for eastern Hudson Bay beluga (*Delphinapterus leucas*). DFO Can. Sci. Advis. Sec. Res. Doc. 2012/168. iii + 31 p.

Doniol-Valcroze, T., Gosselin, J.F., Pike, D., Lawson, J., Asselin, N., Hedges, K., and Ferguson, S. 2015a. Abundance estimates of narwhal stocks in the Canadian High Arctic in 2013. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/060. v + 36 p.

Doniol-Valcroze, T., Gosselin, J.-F., Pike, D., Lawson, J., Asselin, N., Hedges, K., and Ferguson, S. 2015b. Abundance estimate of the Eastern Canada – West Greenland bowhead whale population based on the 2013 High Arctic Cetacean Survey. DFO Can. Sci. Advis. Sec. Res. Doc. 2015/058. v + 27 p.

Doniol-Valcroze, T., Mosnier, A., and Hammill, M.O. 2016. Testing estimators of walrus abundance: insights from simulations of haul-out behaviour. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/040. v + 18 p.

Elliot, R.E, Moulton, V.D., Raborn, S.W. and Davis, R. A. 2013. Hudson Strait marine mammal aerial surveys, 10 March to 2 April. Report prepared by LGL Ltd for Baffinland Iron Mines Corp. 107 p. (LGL Report No. TA8129-2. Prepared by LGL Limited, King City, ON for Baffinland Iron Mines Corporation, Toronto, ON. 87 p.)

Geweke, J. 1996. Evaluating the Accuracy of Sampling-based Approaches to the Calculation of Posterior Moments, *In* Bayesian Statistics 4 Edited by Bernardo, J.M., Berger, J.M., Dawid, A.P., and Smith, A.F.M. Oxford University Press:169–193.

Hammill,M.O. and Stenson, G.B. 2003. Application of the Precautionary Approach and Conservation Reference Points to the management of Atlantic seals: A Discussion Paper. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/067.

Hammill, M.O. and Stenson, G.B. 2007. Application of the Precautionary Approach and Conservation Reference Points to the management of Atlantic seals. ICES J. Mar. Sci. 64: 702–706.

Hammill, M.O. and Stenson, G.B. 2013. A Discussion of the Precautionary Approach and its Application to Atlantic Seals. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/030. v + 25 p.

Hammill. M.O., Mosnier, A., Gosselin, J.-F., Higdon, J.W., Stewart, D.B., Doniol-Valcroze, T., Ferguson, S.H., and Dunn, B. 2016a. Estimating abundance and total allowable removals for walrus in the Hudson Bay-Davis Strait and south and east Hudson Bay stocks. DFO Can. Sci. Advis. Sec.Res. Doc. 2016/036. v + 37 p.

Hammill, M.O., Blanchfield, P., Higdon, J.W., Stewart, D.B., and Ferguson, S.H. 2016b. Estimating abundance and total allowable removals for walrus in Foxe Basin. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/014. iv + 20 p.

Hoyle, S. and Maunder, M. 2004. A Bayesian integrated population dynamics model to analyze data for protected species. Anim. Biodivers. Conserv. 27: 247–266.

Innes, S. and Stewart, R.E.A. 2002. Population size and yield of Baffin Bay beluga (*Delphinapterus leucas*) stocks. NAMMCO Sci. Publ. 4: 225–238.

King, R., Gimenez, O., Morgan, B., and Brooks, S. 2010. Bayesian Analysis for Population Ecology. Chapman & Hall / CRC Press. 442 p.

Lonergan, M. 2011. Potential biological removal and other currently used management rules for marine mammal populations: A comparison. Mar. Policy. 35: 584–589.

Lonergan, M. 2012. The targets of management rules for marine mammal populations require justification: A reply to Cooke et al. Mar. Policy. 36: 1188-1190. doi:10.1016/j.marpol.2012.02.010

Loughrey A.G. 1959. Preliminary investigation of the Atlantic walrus *Odobenus rosmarus rosmarus* (Linneaus). Can. Wildl. Serv. Bull. (Ott.) (Series 1) 14: 123 p.

Lydersen C, Aars, J., and Kovacs, K.M. 2006. Estimating the number of walruses in Svalbard from aerial surveys and behavioural data from satellite telemetry. Arctic, 61: 119–128.

Mansfield, A.W. 1962. Present status of the walrus population at Southampton and Coats islands, pp. 41-52 (No. 16). In H.D. Fisher (in Charge), Fisheries Research Board of Canada, Arctic Unit (Montreal, Quebec), Annual Report and Investigators Summaries, April 1, 1961 to March 31, 1962. [Available online from Fisheries and Oceans Canada libraries]

Mansfield A.W. 1973. The Atlantic walrus *Odobenus rosmarus* in Canada and Greenland. IUCN (Intl Union Conserv. Nat. Nat. Resour.) Publ. New Ser. Suppl. Pap. 39: 69–79.

Mansfield, A.W., and St. Aubin, D.J. 1991. Distribution and abundance of the Atlantic walrus *Odobenus rosmarus rosmarus*, in the Southampton Island-Coats Island region of northern Hudson Bay. Can. Field-Nat. 105: 95–100.

Milner-Gulland, E.J., Shea, K., Possington, H., Coulson, T., and Wilcox, C. 2001. Competing harvesting strategies in a simulated population under uncertainty. Anim. Conserv. 4: 157–167.

Mosnier, A, Doniol-Valcroze, T., Gosselin, J.-F., Lesage, V., Measures, L.N., and Hammill, M.O. 2015. Insights into processes of population decline using an integrated population model: the case of the St. Lawrence Estuary beluga (*Delphinapterus leucas*). Ecol. Model. 314: 15–31.

NAMMCO. 2006. NAMMCO (North Atlantic Marine Mammal Commission) Scientific Committee Working Group on the stock status of walruses in the North Atlantic and adjacent seas. Final Report. Copenhagen, 11-14 January 2005. 27 p.

Orr J.R., Renooy, B., and Dahlke, L. 1986. Information from hunts and surveys of walrus (*Odobenus rosmarus*) in northern Foxe Basin, Northwest Territories, 1982–1984. Can. Manuscr. Rep. Fish. Aquat. Sci. 1899: iv + 29 p.

Pella, J.J., and Tomlinson, P.K. 1969. A generalized stock production model. Bull. Inter-Amer. Tropical Tuna Comm. 13: 420–496.

Plummer, M. 2003. A program for analysis of Bayesian graphical models using Gibbs sampling. in: Proceedings of the 3rd International Workshop on Distributed Statistical Computing. Vienna, Austria.

Schaub, M., and Abadi, F. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. J. Ornithol. 152: 1–11.

Sease, J.L., and Chapman, D.G. 1988. Pacific walrus *Odobenus rosmarus divergens*. In Selected marine mammals of Alaska Species account with research and management recommendations. Edited by J. W. Lentfer. Marine Mammal Commission, Washington, D.C. 275 p.

Stenson, G.B., Hammill, M.O., Ferguson, S., Stewart, R.E.A., and Doniol-Valcroze, T. 2012. Applying the precautionary approach to marine mammals in Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/107. iv + 15 p.

Stewart, R.E.A., and Hamilton, J.W. 2013. Estimating total allowable removals for walrus (*Odobenus rosmarus rosmarus*) in Nunavut using the potential biological removal approach. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/031. iv + 13 p.

Stewart, R.E.A., Hamilton, J.W., and Dunn, J.B. 2013. Results of Foxe Basin walrus (*Odobenus rosmarus rosmarus*) surveys, 2010-2011. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/017. iv + 12 p.

Stewart, D.B., Higdon, J.W., Reeves, R.R., and Stewart, R.E.A. 2014. A catch history for Atlantic walruses (*Odobenus rosmarus rosmarus*) in the eastern Canadian Arctic. NAMMCO Sci. Publ. 9: 219–314.

Taylor B.L., De Master, D.P. 1993. Implications of non-linear density dependence. Mar. Mamm. Sci. 9: 360–371.

Taylor, R.L., and Udevitz, M.S. 2015. Demography of the Pacific walrus (*Odobenus rosmarus divergens*): 1974–2006 Mar. Mamm. Sci. 31: 231–254.

Taylor, B.L., Wade, P.R., De Master, D.P., and Barlow, J. 2000. Incorporating uncertainty into management models for marine mammals. Biol. Cons. 14: 1243–1252.

Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., and Hrovat, Y.N. 2007. Lessons from monitoring trends in abundance of marine mammals. Mar. Mamm. Sci. 23: 157–175.

Trzcinski, M.K., Mohn, R., and Bowen, W.D. 2006. Continued Decline Of An Atlantic Cod Population: How Important Is Gray Seal Predation? Ecol. Appl. 16(6): 2276–2292.

Udevitz, M.S., Jay, C.V., Fischbach, A.S., and Garlich-Miller, J.L. 2009. Modeling haul-out behavior of walruses in Bering Sea ice. Can. J. Zool. 87(12): 1111–1128.

Wade, P. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar. Mamm. Sci. 14: 1–37.

Wade, P. R. 2000. Bayesian Methods in Conservation Biology. Conserv. Biol. 14: 1308–1316.

Witting, L., and Born, E.W. 2005. An assessment of Greenland walrus populations. ICES J. Mar. Sci. 62: 266–284.

Witting, L., and Born, E.W. 2014. Population dynamics of walruses in Greenland. NAMMCO Sci. Publ. 9: 191–218.

Table 1. Abundance observations from Nottingham/Frazer/Salisbury island complex and the Walrus – Coats island complex. The SE of the adjusted number was calculated by combining the variance of the abundance estimates with the variance of proportion hauled out using the Delta method: i.e. $SE_{adj} = s_{adj}\sqrt{\frac{var_1}{y_1^2} + \frac{var_2}{y_2^2}}$

Location / Survey type	Date	Number (SE)	Proportion hauled out (SE)	Adjusted number (SE)	Source
Hudson Strait to Southampton Island	Sept 2014	2144	0.30 (0.173)	7147 (4122)	Hammill et al. 2015
Hudson Strait	Mar-Apr 2012	65		5250 (1681)	Elliot et al. 2013
Walrus-Coats Island-Southampton Island					
Aerial surveys	August 1974	2400 (435)	0.30 (0.173)	8667 (3740)	Loughrey 1975
Aerial/Boat surveys	Aug 1981	2650	0.30 (0.173)	8833 (5094)	Stenvollent 1982
Aerial surveys	July-Aug 1979	2Sk 1491 (Mean=82 S.SE=442)	0.30 (0.173)	2733 (2126)	Stenvollent and St Aubin 1981
Aerial surveys	July –Aug 1977	6-2171 (Mean=65, SE=670)	0.30 (0.173)	2707 (2682)	Stenvollent and St Aubin 1981
Aerial surveys	Aug 1985	757+92	0.30 (0.173)	2830 (1632)	[1]Richard 1993
Aerial surveys	July 1989	1231+97	0.30 (0.173)	4427 (2553)	[1]Richard 1993
Aerial surveys	Aug 1990	1373+401	0.30 (0.173)	6113 (3526)	[1]Richard 1993

[1] Richard, P.R. 1993. Summer distribution and abundance of walrus in northern Hudson Bay, western Hudson Strait and Foxe Basin: 1985-1990. AFSAC meeting 17-19 February 1993. Background report. 21 p.

Table 3. Survey year, count/estimate, proportion of animals tagged (pt), and calculated counts for sperm in Prince Basin. Source where the original count data can be found. pbr shows value calculated as outlined in Hammond et al. (2013b). The SE of the abundance number was calculated by combining the variance of the abundance estimates with the variance of proportion tracked via using the Delta method: $se_{N_{pbr}} = N_{pbr}\sqrt{\frac{var(n_t)}{n_t^2} + \frac{var(p_t)}{p_t^2}}$

Year	Number (N)	SE (N)	Proportion tracked (p_t)	SE (p_t)	pbr abundance	SE	Source
1983	3,703		0.37	0.15	7,897	3,165	Gilmore et al. (1989)
1989	5,128	4,368	0.37	0.15	10,935	10,205	Richards (1993)
1989	5,515	1,849	0.37	0.15	10,935	7,824	Richards (1993)
2010	3,851		0.37	0.15	10,435	4,013	Stewart et al. (2013)
2011	5,905		0.37	0.15	16,082	6,445	Stewart et al. (2013)
2011	4,456		0.37	0.15	12,119	5,041	Stewart et al. (2013)
2011	(4,454-5,645)2	1033	0.37	0.15	14,000	6,704	(2011 data combined)

[1] Richards, P.R. 1993. Summer distribution and abundance of cetacea in northern Hudson Bay, western Hudson Strait and Foxe Basin, 1988-1989. NAMMCO. ...meeting, 17-19 February 1993. Background report. 21 p.

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[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

Table 2.1: Plant classifications, associations and basic assumptions used in Canada's Plant Hardiness Zones (PHZ) system. Zone 1a is the coldest and zone 11b is the warmest. Each zone is subdivided into two half zones (a and b). Zone boundaries are based on the average annual extreme minimum temperature over a 30-year period (1961–1990). See Figure 2.1 for a map of the zones.

Characteristics	Variables	Plant classifications	Cluster specifications	Criteria
Woody plants (A)	A_1	Large (tall trees)	$\geq$ 10 m	1
			< 10 m	0
Deciduous (winter)	L_1	Deciduous	Yes	1 or 0.5
			No	0
Woody plants (B)	B_1	Large (tall trees)	$\geq$ 10 m	1
			< 10 m	0
Deciduous (Winter)	L_1	Deciduous	Yes	1 or 0.5
			No	0
Woody, deciduous (no foliage in winter)	D	Deciduous	D_{Yes}	1
			D_{No}	0
Woody (evergreen)	W_1	Woody	Yes	1
			No	0
Orchid association	O_{Yes}	Orchids	O_{Yes}	10,000
			O_{No}	0
Carnivory apparent	C	Carnivory	C_{Yes}	10,000
			C_{No}	0
Maximum overall score	S_{max}			1.45

Table 8a. Model outputs for the Hudson Bay-Davis Strait stock using all aerial survey and harvest data (Run 1). Mean, Standard deviation (SD), median, 25th and 75th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a habitat proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N eff is the number of effective chains after considering autocorrelation.

			Quantiles						
	Mean	SD	2.5%	25%	50%	75%	97.5%	R-hat	N eff
K	1,236611	69080	710211	913852	917359	1465117	3246117	1.0002	26000
K prior	1777548	998548	139502	911537	1777559	2654602	3481463	1.0001	1200000
Theta	3.3	1.6	1.1	2.0	3.0	4.5	6.7	1.0001	196000
Theta prior	4.0	1.7	1.1	2.5	4.0	5.5	6.8	1.0001	1200000
Deviance	162.6	2.5	159.3	160.9	162.1	163.8	169.0	1.0001	1200000
Proc. process	10322.9	1228	1086.4	6080.7	11185.8	20358.5	46194.3	1.0001	359000
Proc. process prior	16928.7	1226	1087.2	6827.3	11187.2	20358.9	46777.4	1.0001	1200000
Proc. auto	0.4	2.6	2.3	4.5	6.0	7.9	12.5	1.0001	1200000
Proc. auto prior	6.2	3.9	1.0	3.3	5.4	8.3	16.0	1.0001	1200000
Startpop	1084221	35153	849115	778311	948511	1119119	1186038	1.0001	59000
Startpop prior	1152191	85535	1238	786522	1152039	2225772	2992660	1.0001	6730000
Struck and lost	0.35	0.15	0.09	0.23	0.33	0.45	0.68	1.0001	1200000
Struck and lost prior	0.49	0.17	0.12	0.36	0.42	0.58	0.78	1.0001	1200000
N2014	69983	15481	41337	59858	68579	77348	107753	1.0001	1400000

Table 6b. Model outputs for the Hudson Bay-Davis Strait stock excluding surveys flown before 1988 (Run 2). Mean, Standard deviation (SD), median, 25th and 75th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation

			Quantiles						
	Mean	SD	2.5%	25%	50%	75%	97.5%	Rhat	n.eff
K	11430	5006	7038	8573	9954	12038	28899	1.0	3700.0
K.prior	17816	9934	1373	9259	17877	26421	34121	1.0	30000.0
Theta	3.4	1.8	1.1	1.8	3.1	4.9	6.8	1.0	22000.0
Theta.prior	4.0	1.7	1.2	2.5	4.0	5.5	6.9	1.0	50000.0
Deviance	88.9	2.4	86.1	87.2	88.3	89.9	95.3	1.0	39000.0
Prec.process	1506	1231	109	612	1190	2055	4724	1.0	50000.0
Prec.process.prior	1510	1238	109	606	1184	2065	4717	1.0	50000.0
Prec.surv	7.4	3.6	2.0	4.7	6.8	9.4	15.8	1.0	50000.0
Prec.surv.prior	6.2	4.0	1.1	3.3	5.4	8.3	16.0	1.0	50000.0
Startpop	9458	1832	6710	8082	9171	10585	13611	1.0	35000.0
Startpop.prior	15336	8517	1265	7993	15383	22712	29306	1.0	50000.0
Struck.and.lost	0.38	0.17	0.09	0.25	0.37	0.5	0.74	1.0	50000.0
Struck.and.lost.prior	0.43	0.17	0.12	0.3	0.42	0.55	0.78	1.0	50000.0
N2014	7437	1576	4579	6524	7387	8240	10737	1.0	33000.0

Table 6c. Model outputs for the Hudson Bay-Davis Strait stock including all surveys but harvests from east Baffin Island are excluded (Run 3). Mean, Standard deviation (SD), median, 25th and 75th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation

			Quantiles						
	Mean	SD	0.025	0.25	0.5	0.75	0.975	Rhat	n.eff
K	8076.6	2918.5	5676.4	6756.3	7529.8	8509.2	14934.3	1.001	16000
K.prior	17735.5	9969.1	1366.8	9085.7	17720.2	26359.8	34136.4	1.001	220000
Theta	3.2	1.6	1.1	1.8	2.8	4.3	6.7	1.001	67000
Theta.prior	4.0	1.7	1.1	2.5	4.0	5.5	6.9	1.001	220000
deviance	162.1	2.3	159.3	160.4	161.5	163.2	167.9	1.001	220000
prec.process	1499.7	1225.7	109.6	606.1	1184.0	2052.1	4654.9	1.001	210000
prec.process.prior	1501.4	1228.7	106.0	605.2	1181.7	2058.1	4677.0	1.001	220000
prec.surv	6.6	2.7	2.5	4.7	6.3	8.2	12.8	1.001	220000
prec.surv.prior	6.3	4.0	1.0	3.3	5.4	8.3	16.1	1.001	120000
Startpop	7446.3	1156.8	5510.9	6598.2	7328.1	8191.1	9959.0	1.001	220000
Startpop.prior	17739.9	9962.7	1361.5	9115.8	17739.0	26381	34136.1	1.001	220000
struck.and.lost	0.43	0.17	0.13	0.30	0.42	0.54	0.76	1.001	220000
struck.and.lost.prior	0.43	0.18	0.12	0.30	0.42	0.55	0.78	1.001	220000
N2014	6356	1006	4634	5784	6288	6821	8496	1.001	190000

Table 7. Model outputs for the Foxe Basin stock. Mean, Standard deviation (SD), median, 25th and 75 th quantiles and 95% credibility intervals (2.5%, 97.5%) for model parameters: carrying capacity (K), density dependent shape (theta), process error, survey precision, starting population, struck and loss, and population size in 2014 for the Hudson Bay-Davis Strait stock assuming a haulout proportion of 0.3 (SE=0.173). R-hat is the BGR statistic, values near 1 indicate convergence of chains. N.eff is the number of effective chains after considering autocorrelation.

			Quantiles						
	Mean	SD	2.5%	25%	50%	75%	97.5%	R-hat	N.eff
K	13583	2770	9466	11812	13195	14853	20030	1.00	120000
K.prior	20234	11383	1502	10384	20202	30115	38980	1.00	120000
Theta	3.4	1.4	1.1	2.4	3.4	4.4	6.3	1.01	120000
Theta.prior	3.4	1.4	1.1	2.4	3.4	4.4	6.3	1.01	40000
Deviance	96.88	2.03	94.53	95.41	96.39	97.81	102.11	1.00	100000
Prec.process	1497	1222	106	606	1182	2050	4663	1.00	10000
Prec.process.prior	1506	1225	109	611	1189	2064	4678	1.00	120000
Prec.surv	7.87	3.71	2.36	5.16	7.30	9.97	16.66	1.00	120000
Prec.surv.prior	6.24	3.95	1.03	3.34	5.42	8.27	16.05	1.00	120000
Startpop	11862	3297	4604	10229	12205	13905	17881	1.001	120000
Startpop.prior	20242	11402	1499	10345	20226	30168	39032	1.001	32000
Struck.and.lost	0.330	0.178	0.051	0.190	0.309	0.450	0.711	1.001	120000
Struck.and.lost.prior	0.334	0.178	0.052	0.194	0.315	0.455	0.717	1.001	120000
N2014	12489	2537	8574	10853	12158	13701	18489	1.00	120000

FIGURES

Figure 1. Location of Atlantic walrus stocks as identified by management units in the eastern Canadian Arctic. The stocks are Baffin Bay (AW-01), West Jones Sound (AW-02), Penny Strait-Lancaster Sound (AW-03), North and Central Foxe Basin stocks (AW-04), Hudson Bay-Davis Strait and South and East Hudson Bay stocks.

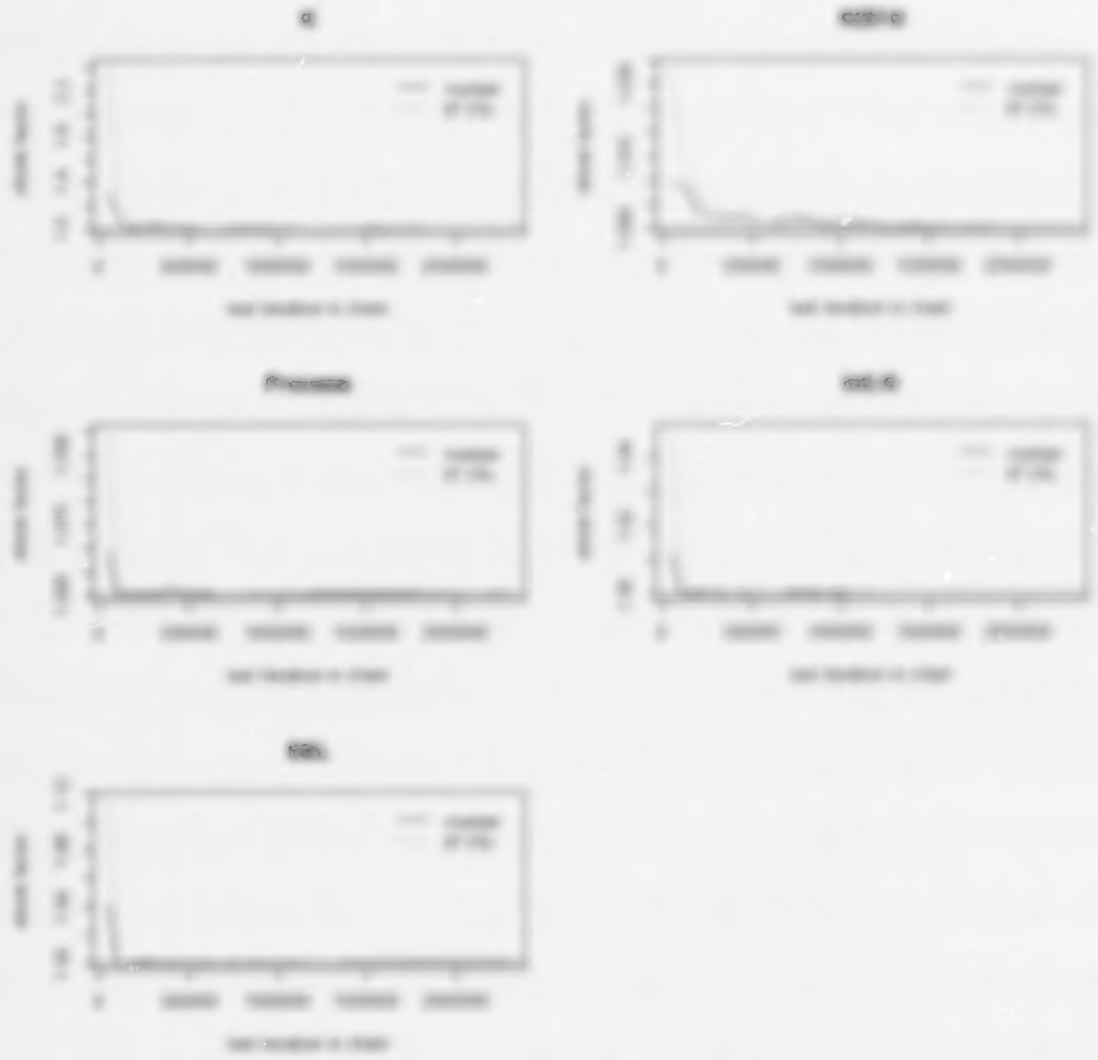


Figure 3a. BASP convergence diagnostic for carrying capacity (K), population size in 2014 (N_{2014}), Process error, initial population (init.N) and Ricker and Logit ($Ricker_a$) for the five chains plotted for increasing numbers of iterations (up to 1 000 000). Values close to 1 indicate good convergence for the Hawkesbury Bay-Clavis Small stock.

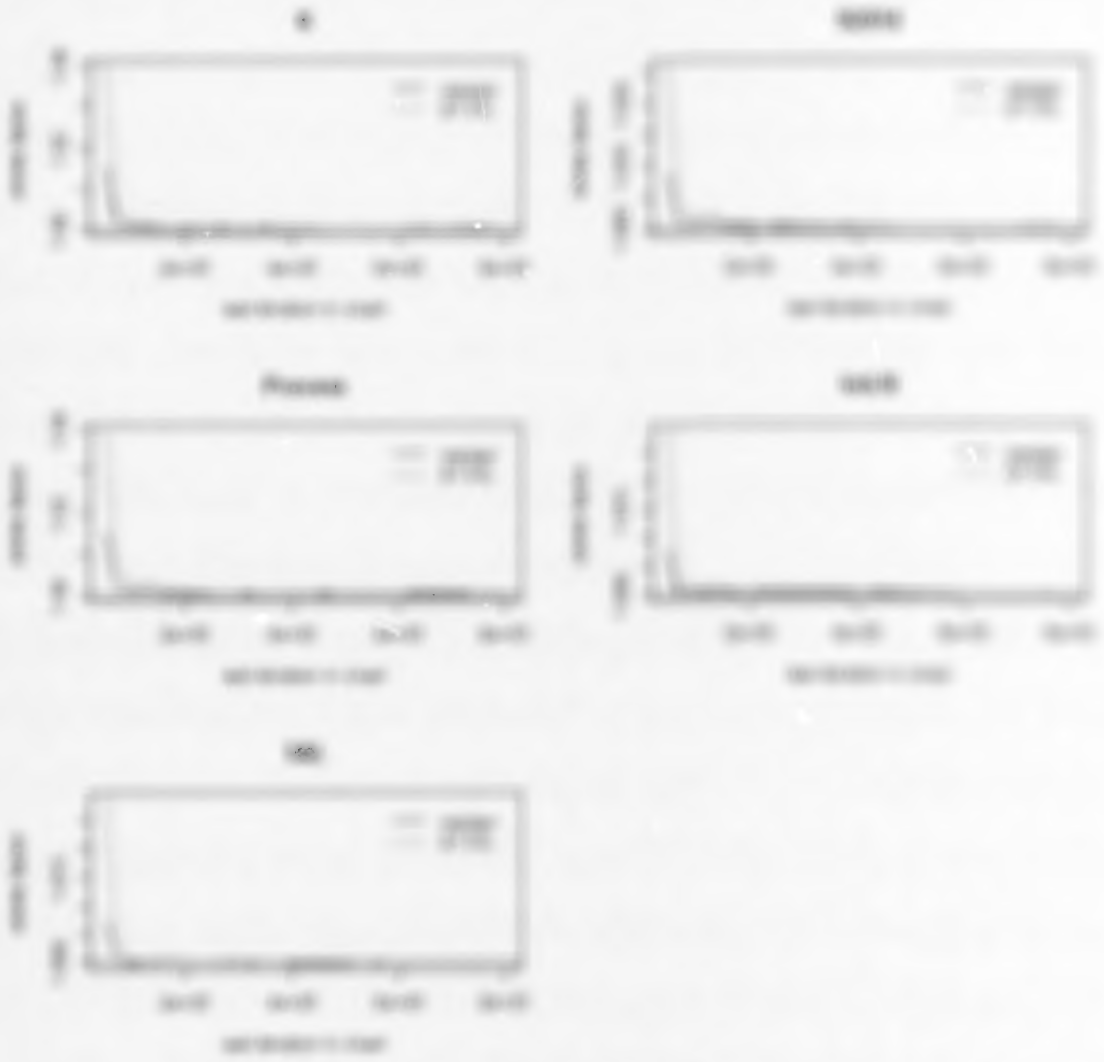


Figure S4. ECDF convergence diagnostic for the Pond Basin shrub–soil feedback ensemble using a fractional proportion of 0.37. Variables shown include carrying capacity (K), population rate (r, 0.11), epsilon (ε), process error, initial population (x0 = 8), and delta (δ), and the log-likelihood (obj). Curves plotted for increasing numbers of iterations (up to 1,000,000). Values close to 1 indicate good convergence.

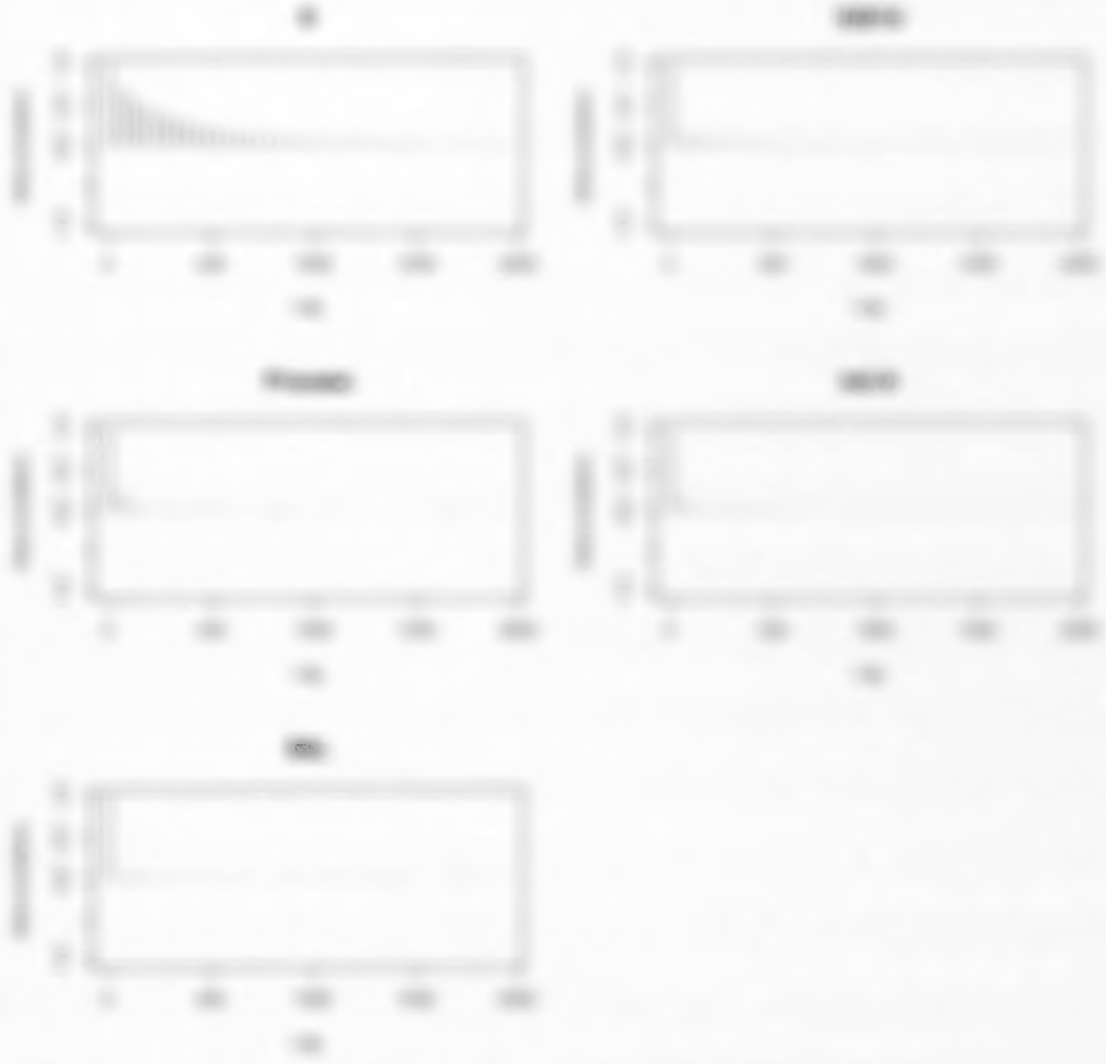
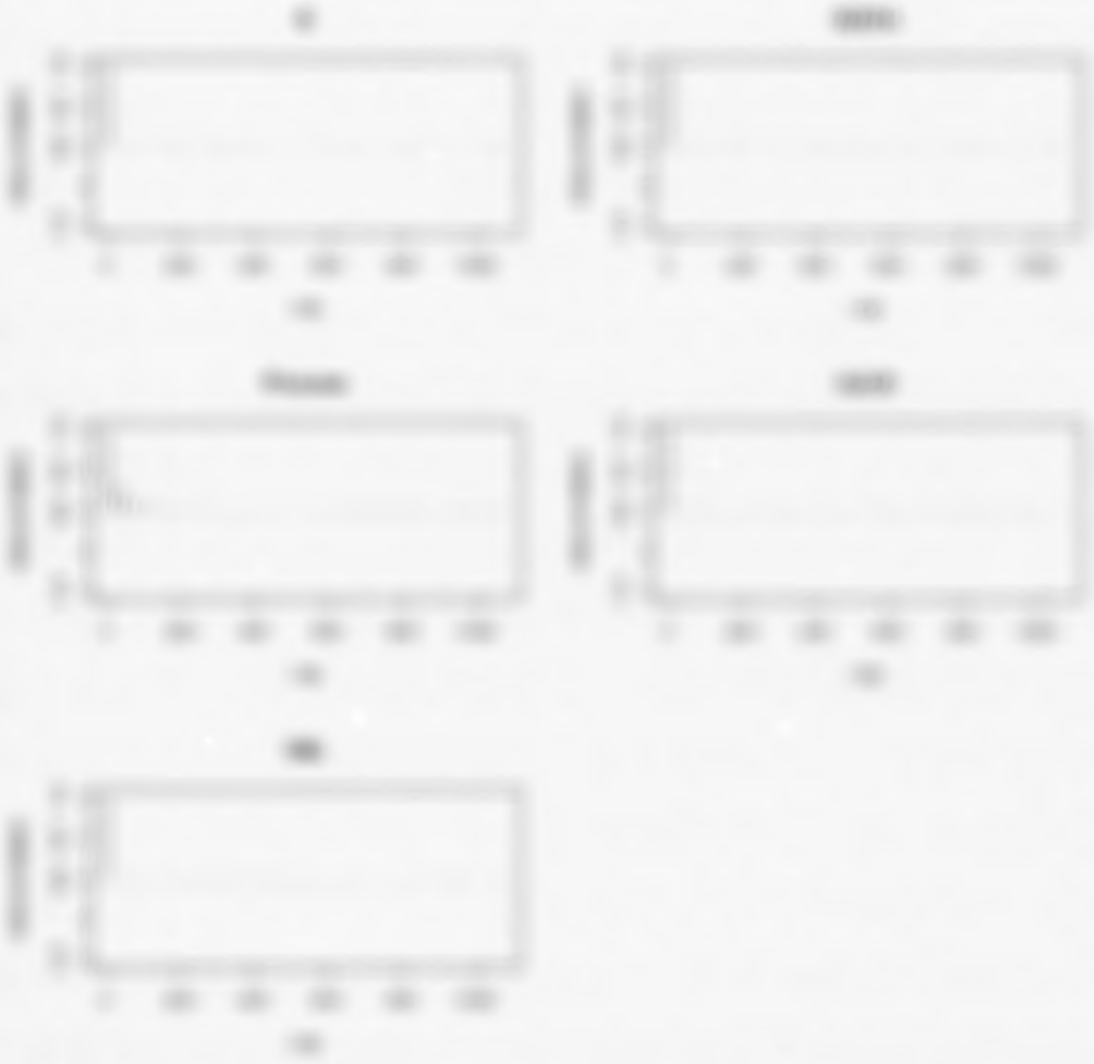


Figure 3a. Plots showing evidence for each correlation within each class for simulated recovery-rate (ρ), SSR population scaling (SSR(t)), process error, within-population case size (k) and annual case-load (SIS). See text Section 'Map charts' (Small) above.


Ar
Ethanol
Propane
Methane
Air
Pressure (bar)
Time (s)

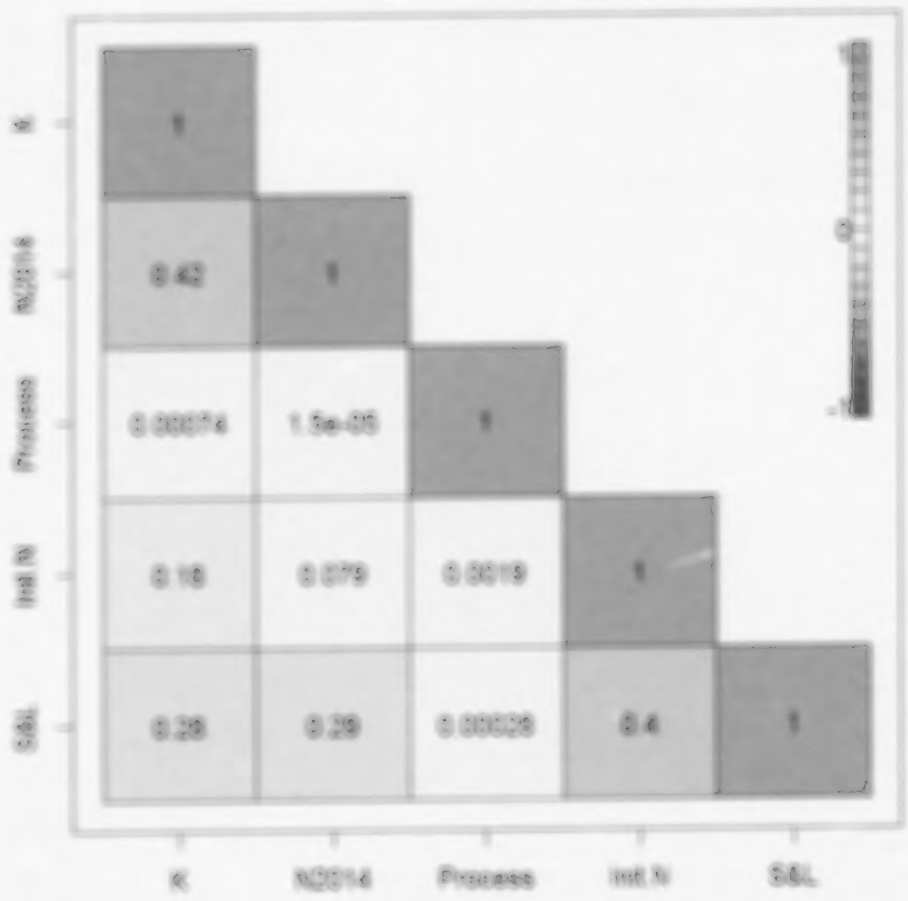


Figure 5a. Hudson Bay-Davis Strait stock model runs that included all survey data and reported harvests from all communities. Correlations are shown between model parameters carrying capacity (K), the 2014 population estimate (N2014), process error (Process), initial population size (Init N), and struck and lost (S&L).

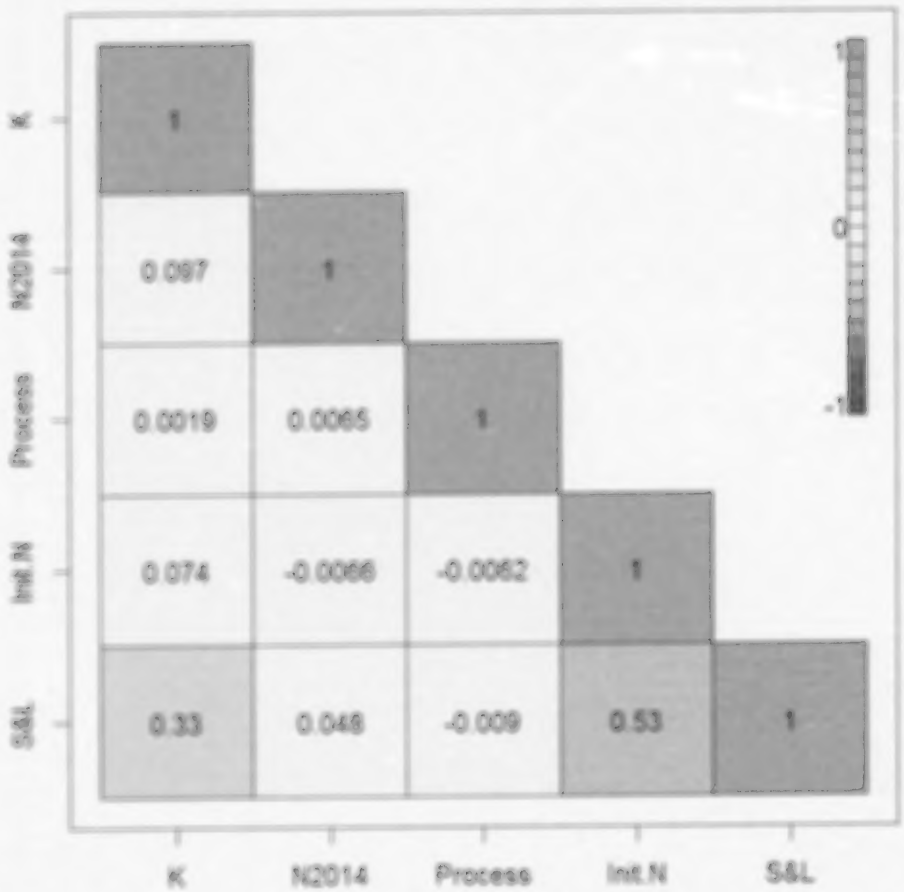


Figure 5b. Hudson Bay-Davis Strait stock model run with surveys flown before 1988 excluded. Correlations are shown between model parameters for variables carrying capacity (K), 2014 population estimate (N2014), process error (Process), initial population size (init.N) and struck and lost (S&L).

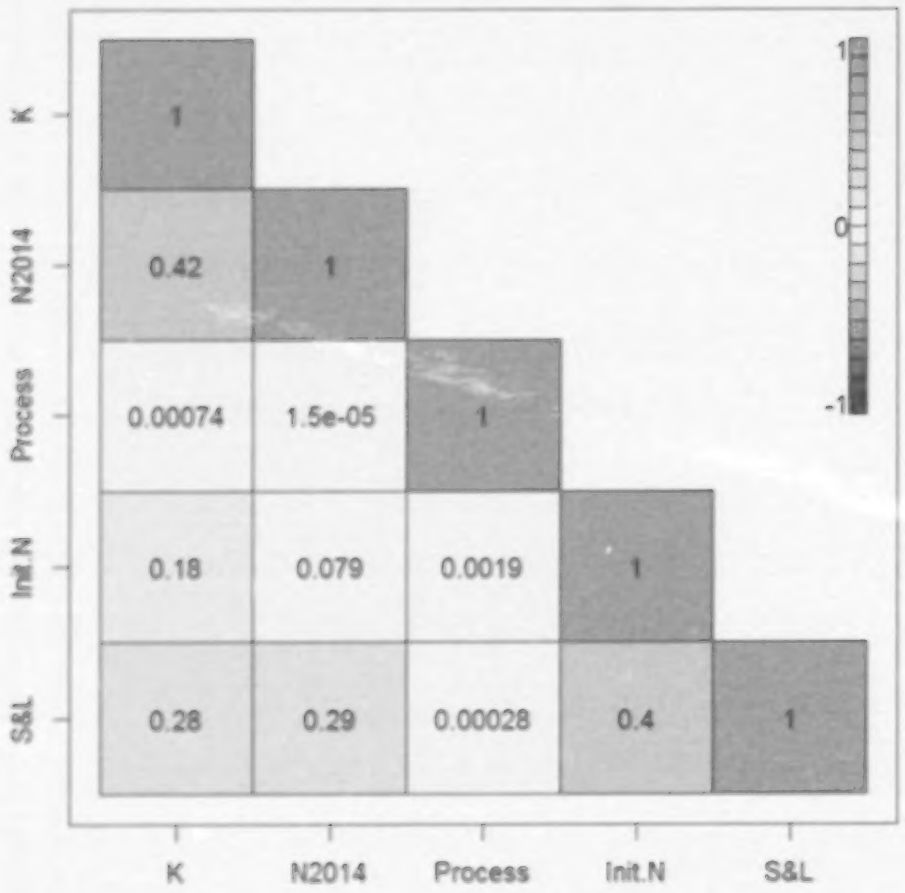


Figure 5c.Hudson Bay-Davis Strait model run with harvests from east Baffin excluded. Correlations are shown between model parameters for variables carrying capacity (K), 2014 population estimate (N2014), process error (Process), initial population size (init.N) and struck and lost (S&L).

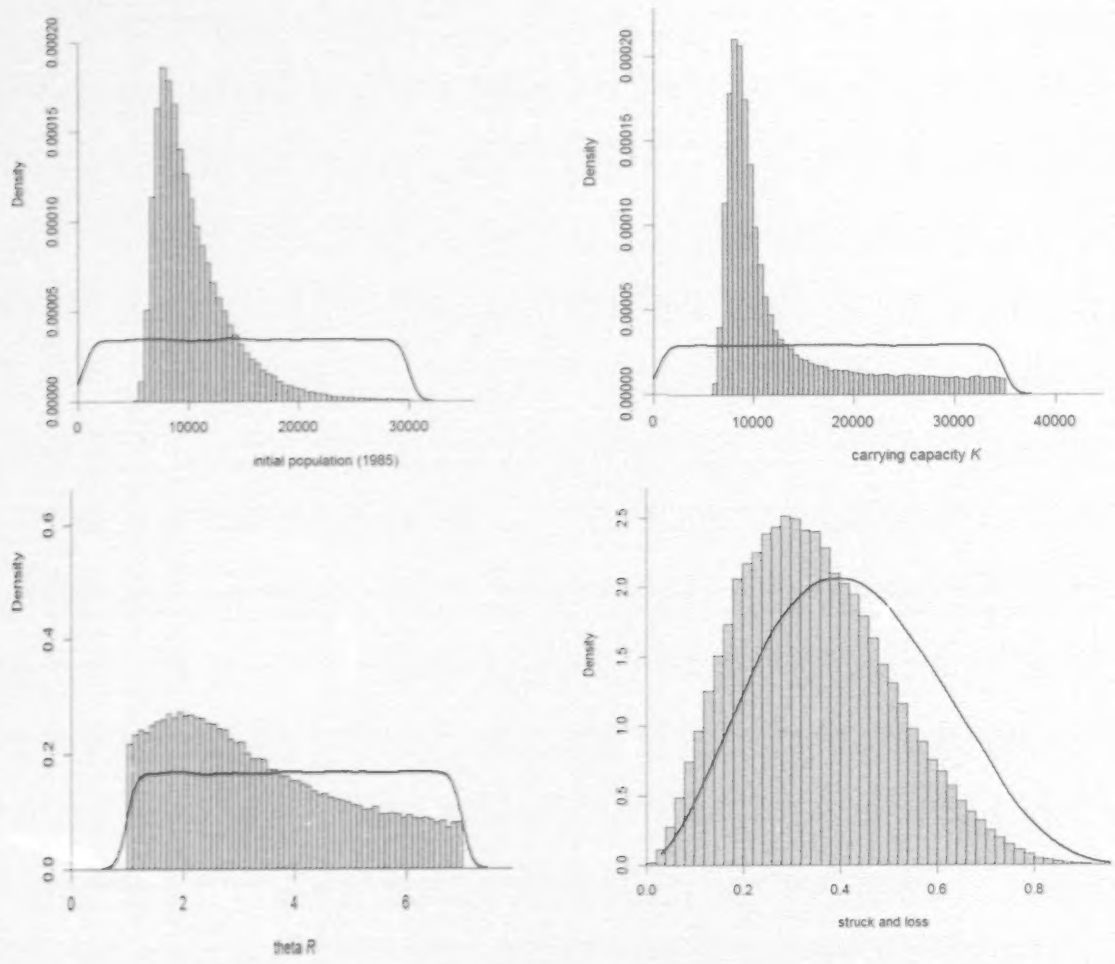


Figure 6a. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Hudson Bay-Davis Strait stock model run that included all surveys and harvests from all communities. The prior for the process error was not updated and is not shown. Prior and posterior means. Quantiles and 95% Credibility Intervals are shown in table 6a.

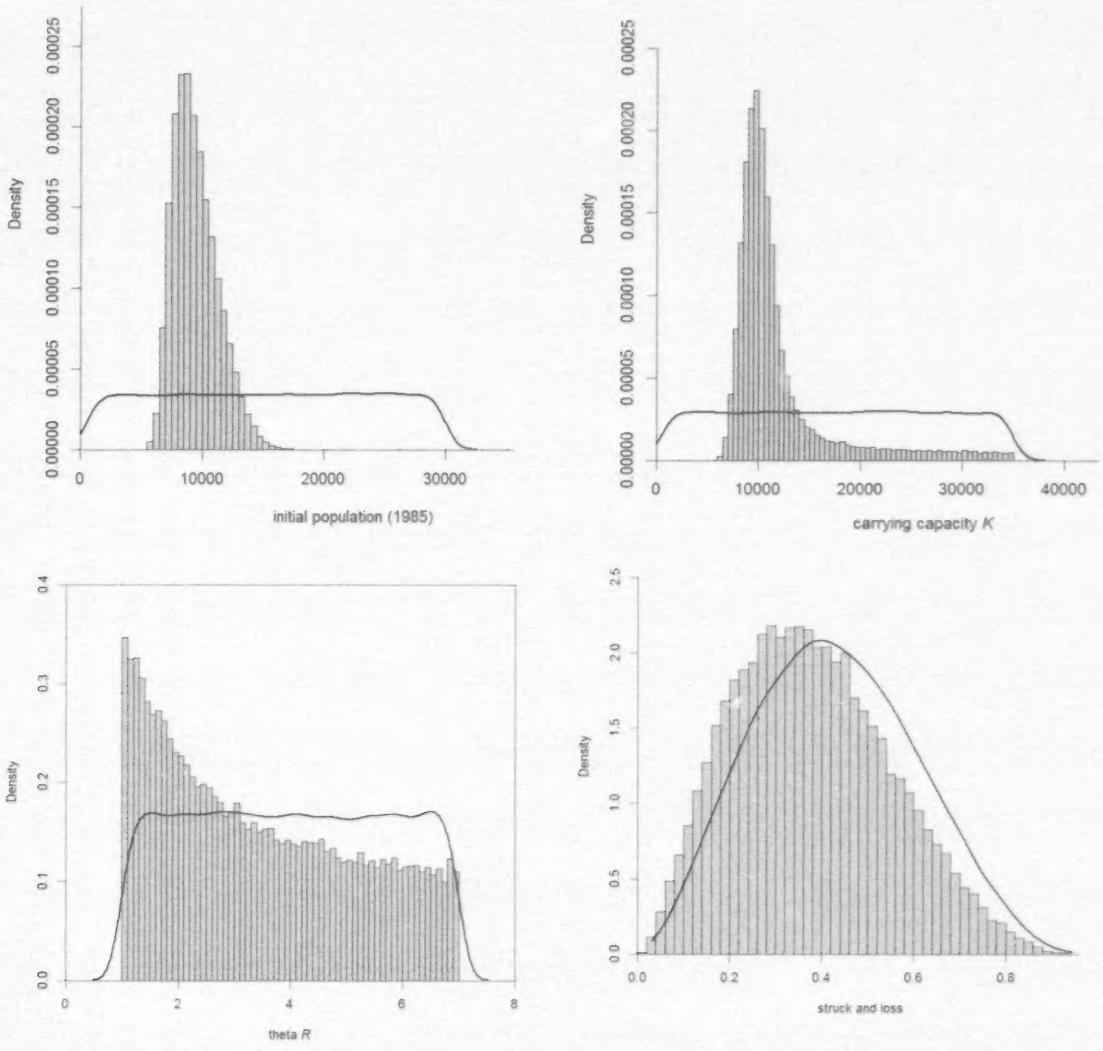


Figure 6b. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Hudson Bay-Davis Strait stock for the run that did not include surveys flown before 1988. The prior for the process error was not updated and is not shown. Prior and posterior means. Quantiles and 95% Credibility Intervals are shown in table 6b.

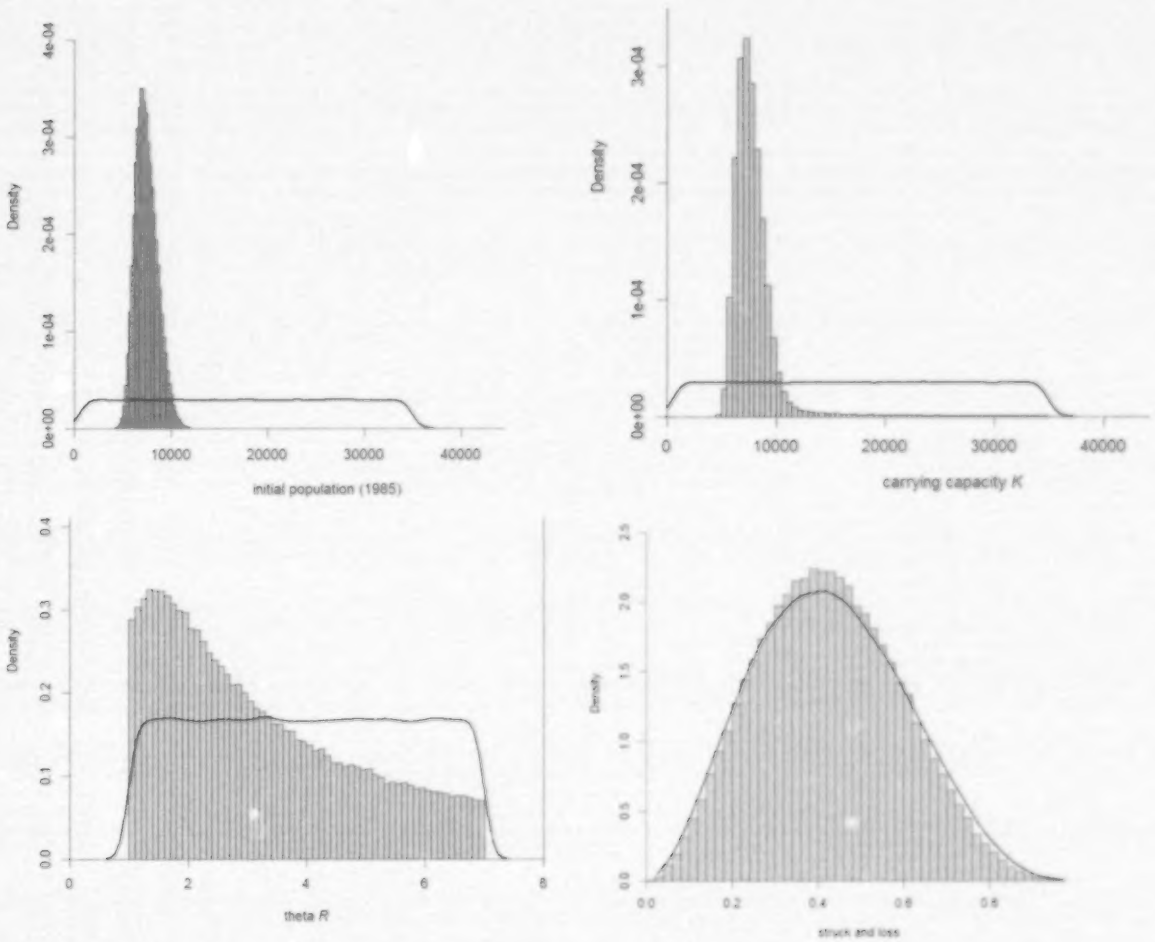


Figure 6c. Prior (lines) and posterior (bars) distributions of four parameters estimated by the model for the Hudson Bay-Davis Strait stock for the run that did not include harvests from east Baffin Island. The prior for the process error was not updated and is not shown. Prior and posterior means. Quantiles and 95% Credibility Intervals are shown in table 6c.

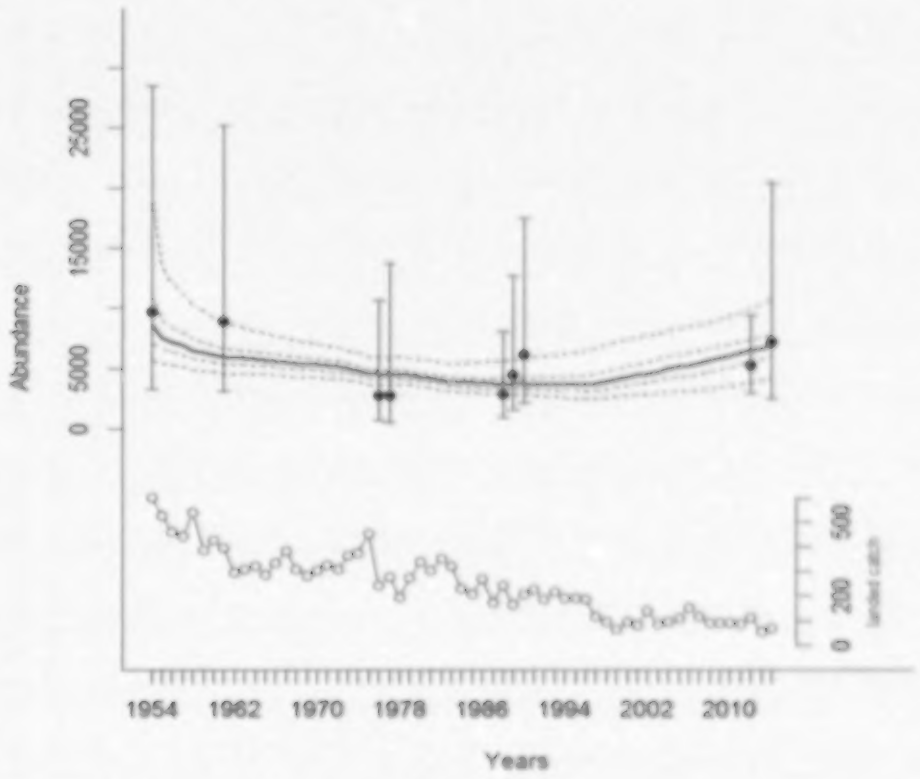
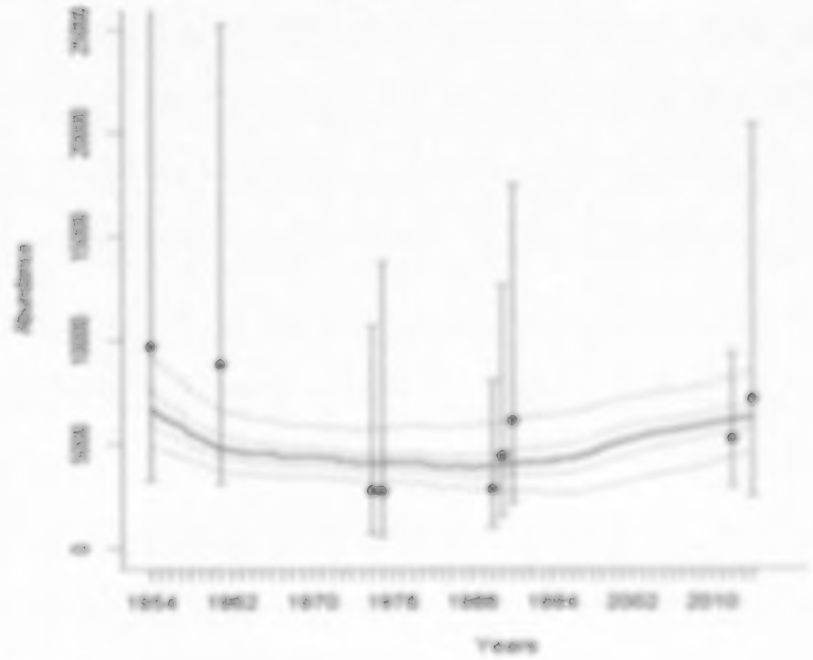


Figure 7a. Estimates of Hudson Bay-Davis Strait walrus abundance obtained by fitting the model to all aerial survey estimates. Solid line: median estimates. Inner dashed lines: 25% and 75% quantiles. Outer dashed lines: 2.5% and 97.5% quantiles (= Bayesian Credible Interval). The model was fitted to aerial survey estimates corrected for animals at the surface (closed circles. ± 95% confidence intervals). Right y-axis: Reported catch of walrus from Ungava Bay, Hudson Strait, northeastern Hudson Bay, Southampton Island and northwestern Hudson Bay communities (open circles). For communities with missing data, the average of the most recent five years of catches was substituted.



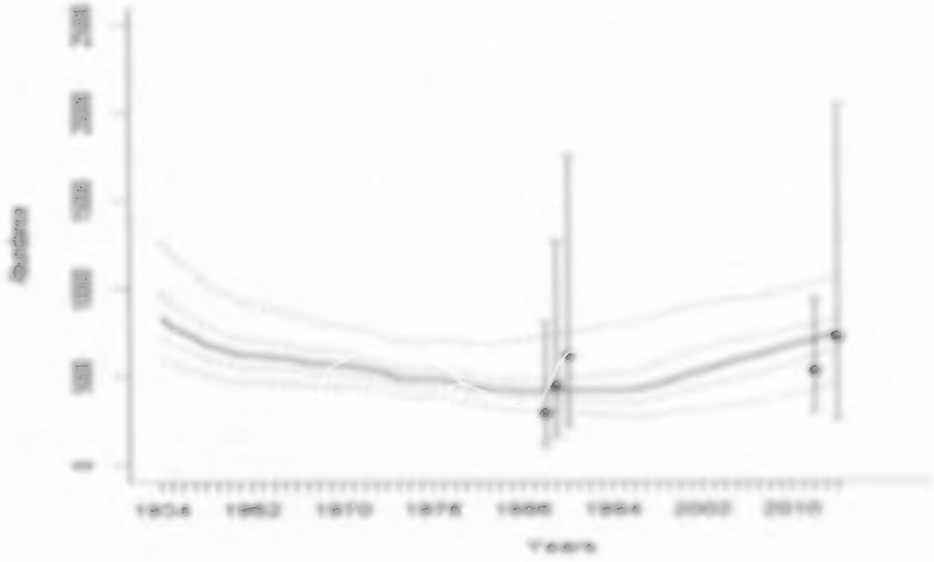


Figure 7b. Model estimates of Hudson Bay-Davis Strait walrus abundance taking into account all harvests and all aerial surveys (top) or if surveys prior to 1968 are excluded from the model (bottom). Solid line: median estimates. Inner dashed lines: 25% and 75% quantiles. Outer dashed lines: 2.5% and 97.5% quantiles (= Bayesian Credible Interval). Aerial survey estimates are corrected for animals at the surface (closed circles, ± 95% CL).

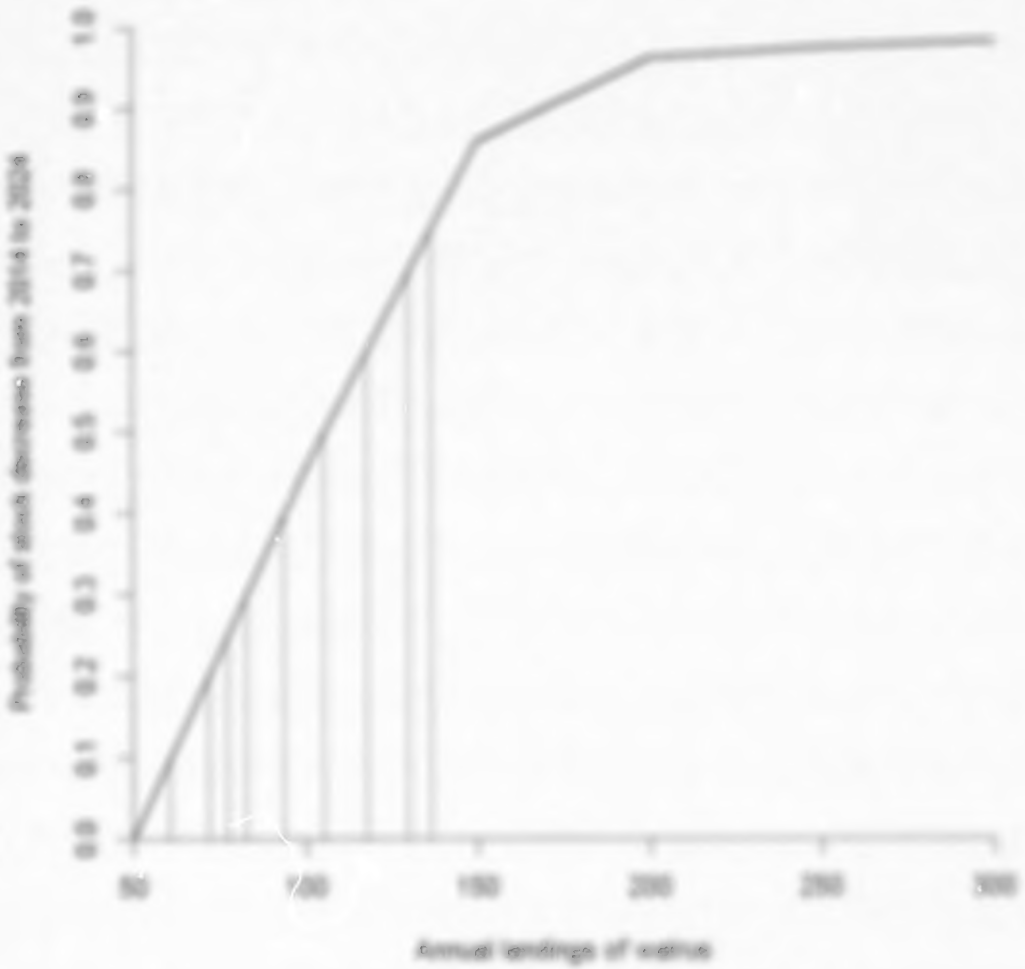


Figure 6. Probability of Hudson Bay-Davis Strait walrus stock decrease from the 2014 abundance estimate after ten years of harvest estimated by a stochastic Bayesian stock-production model, as a function of the number of reported walruses removed from the stock every year. Dotted lines indicate levels of harvest (x-axis) corresponding to the probability of decline (y-axis).

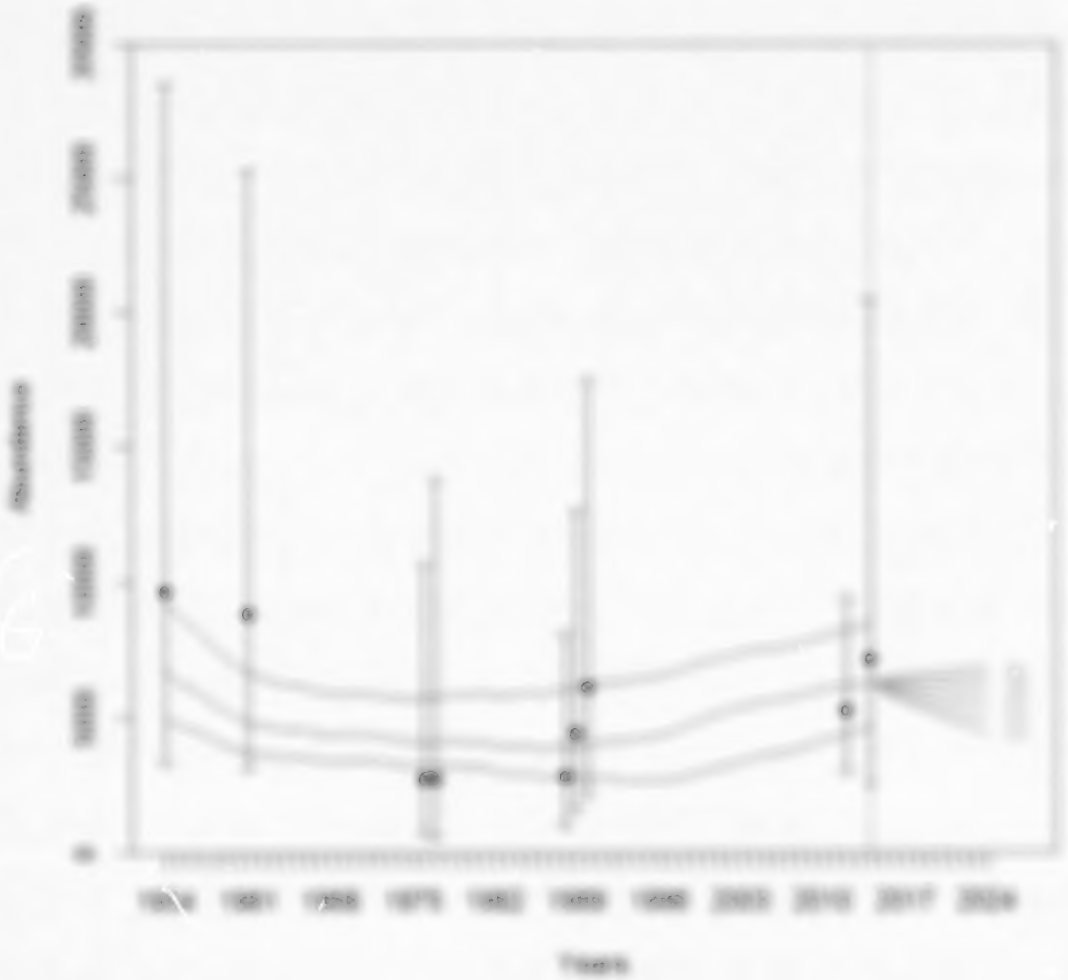


Figure 8. Model estimates of the Hudson Bay-Davis Strait walrus stock abundance and predicted trends in median population size if the same reported harvest (0, 50, 100, 150, 200, 250 or 300 animals) is removed annually over the next 10 years. Middle line is the median estimate. The outer black lines represent the 95% Credibility intervals. Aerial survey estimates are corrected for animals at the surface (closed circles, ± 95% CL).

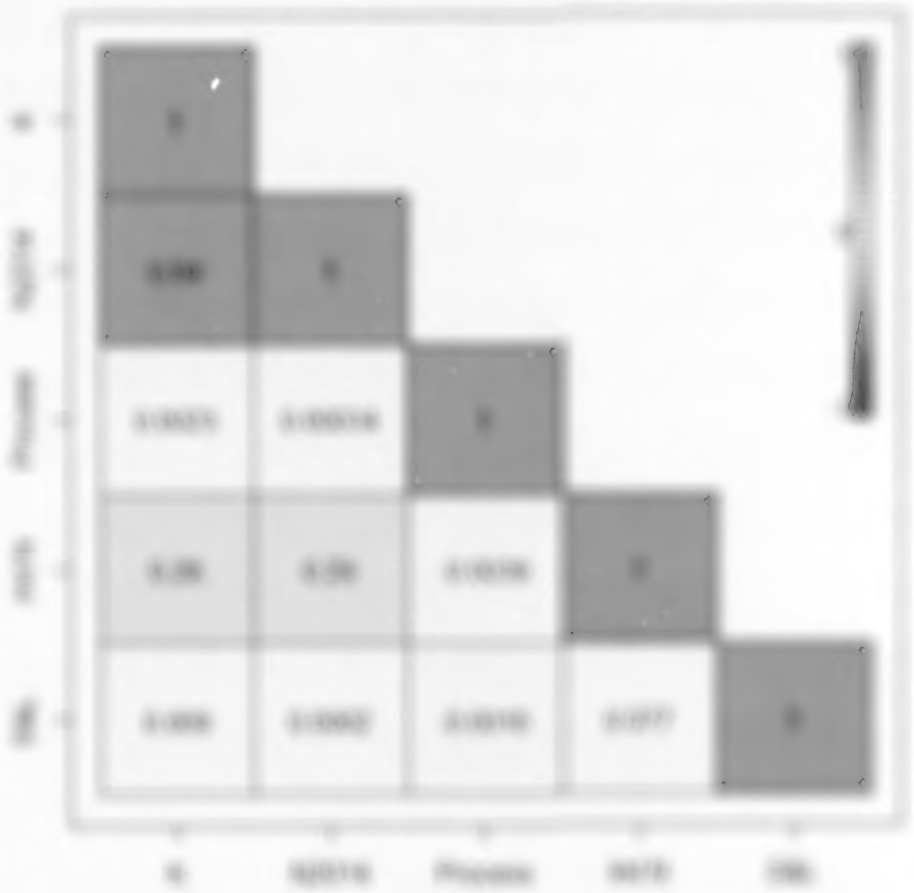
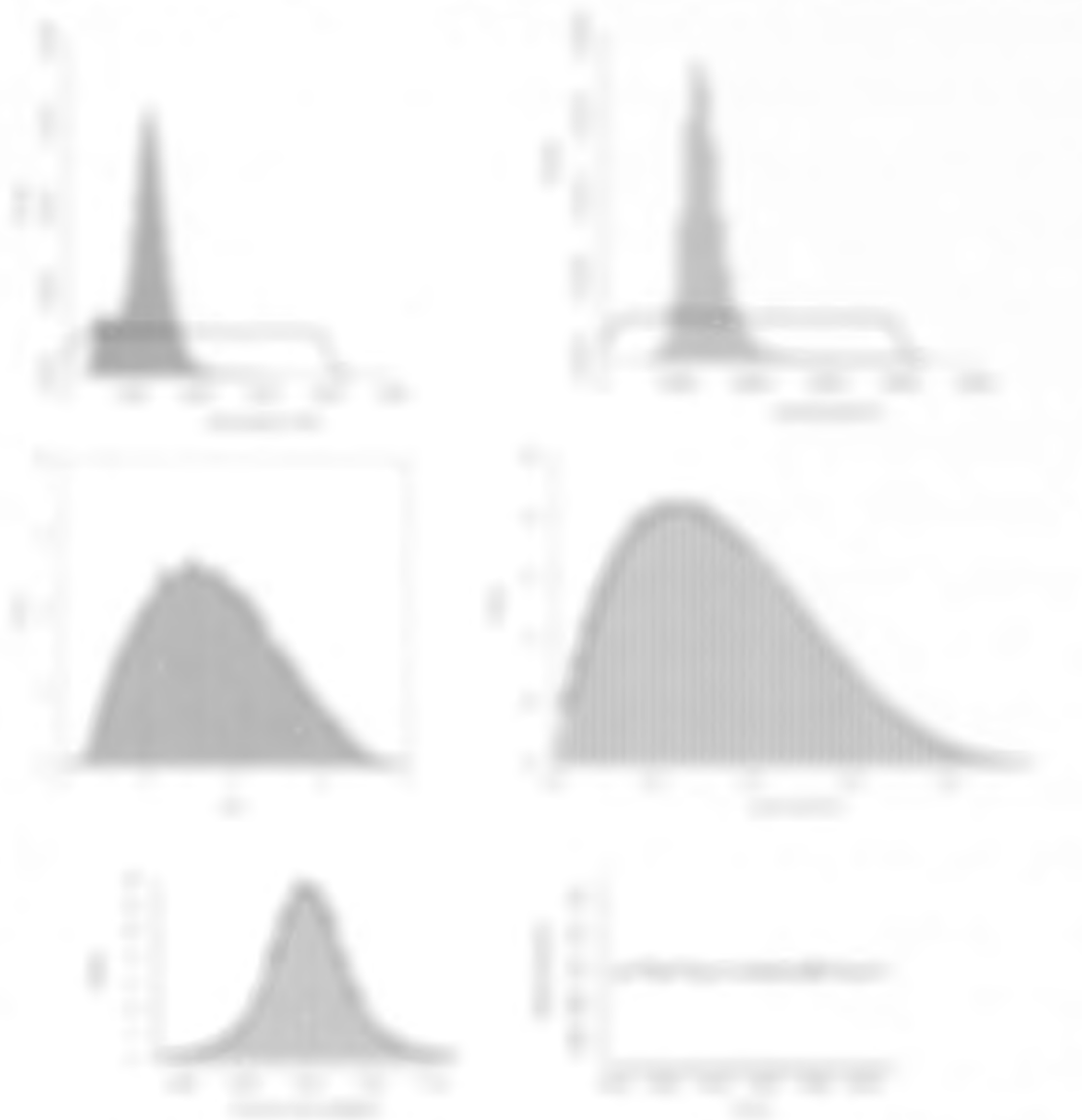


Figure 10. Four-facet stock model runs that included all survey SMA and WASHFA, event 0101 all simulations. Correlations (as shown between model parameters) showing (going A) the SZ10 population estimate, W3016, process error (Process), initial population size (K) and stock and fuel (Obs). Residual month were adjusted removing a proportion of 0.10 (F 2.76) population size (residual



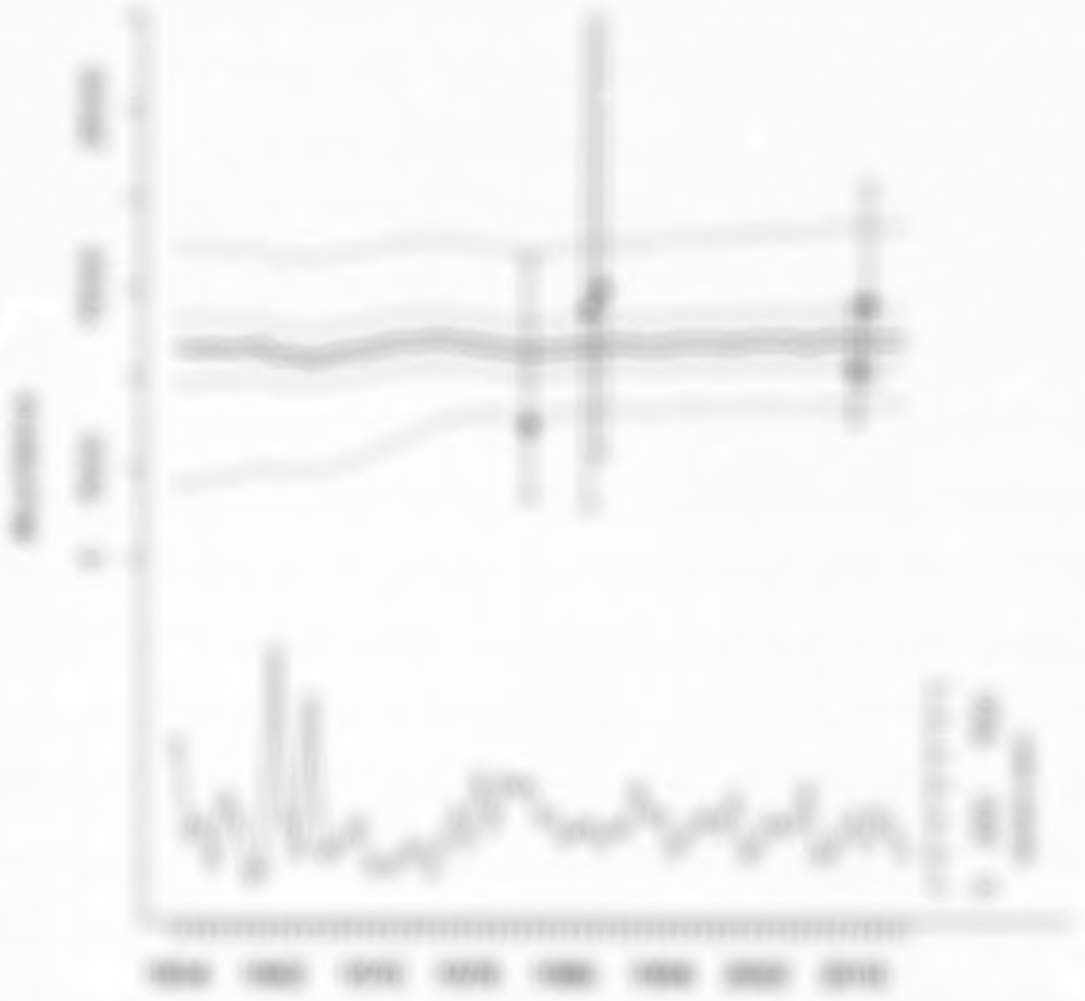


Figure 3. Model estimates of Frog Mesic pattern recruitment, calculated annually from the probability of all candidate models in set (see Table 2). Solid line, annual estimate; dotted lines, 95% CI. The asymptotic Ricker function (see Table 2) fit the data best. Recruitment is plotted against the number of adult females in the previous year. Open circles, years in which recruitment was below the 95% CI of the asymptote; closed circles, years in which recruitment was above the 95% CI of the asymptote. Arrows connect successive years. Numbers next to arrows indicate the year of the earlier of the two years. The 1999 point is the most recent year for which data are available, and the 2000 point is the first year for which we have data on recruitment. Because the 1999 point is above the asymptote, we predict that recruitment will increase in 2000. Because the 2000 point is below the asymptote, we predict that recruitment will decrease in 2001. Note that the 1999 point is the only point that is above the asymptote, and the 2000 point is the only point that is below the asymptote. Thus, we predict that recruitment will increase in 2000 and decrease in 2001. Because the 2000 point is the only point that is below the asymptote, we predict that recruitment will increase

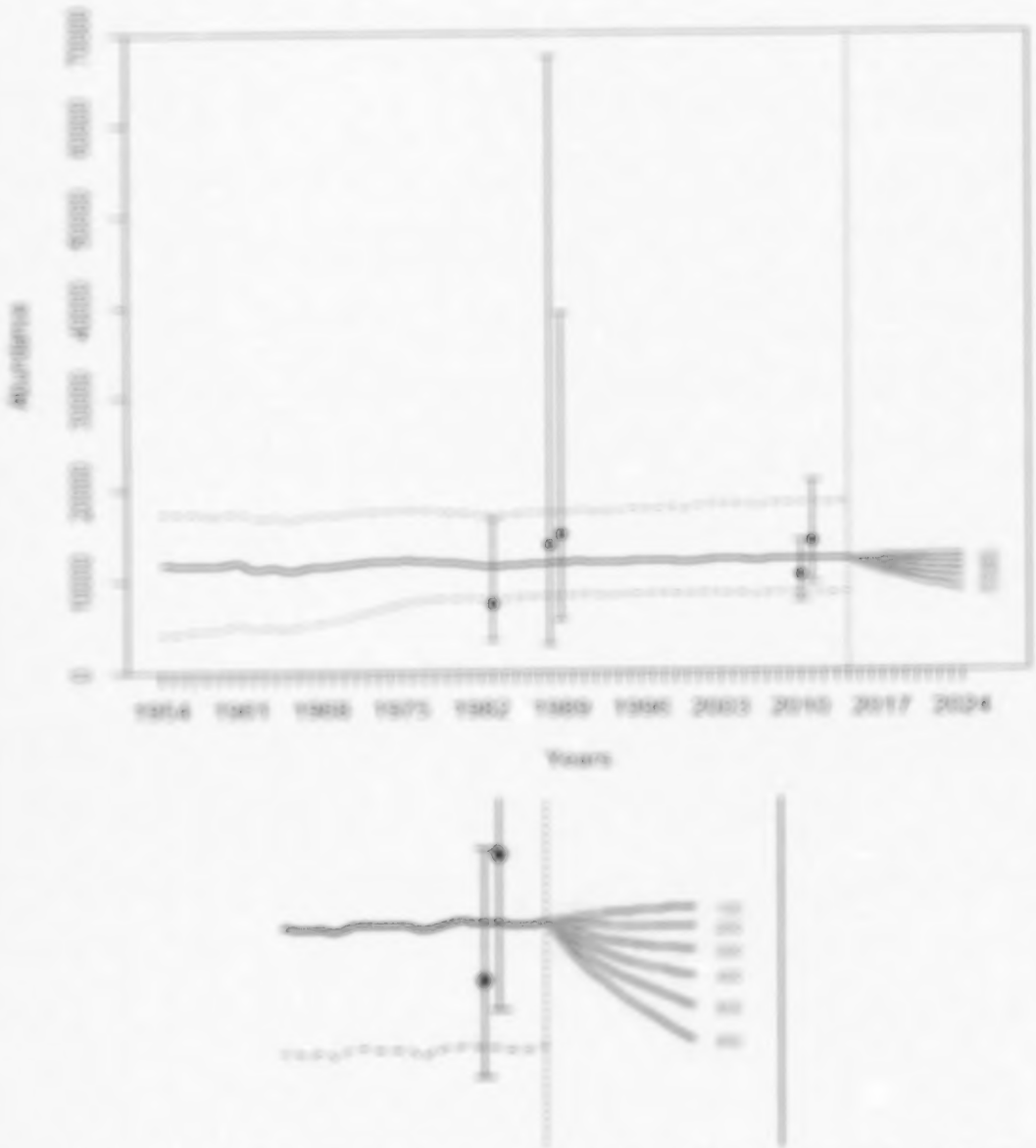


Figure 14. Model estimates of the Foxe Basin walrus population (adjusted assuming that the proportion of the population hauled out was 0.37) and predicted trends in median population size if the same reported harvest (100, 200, 300, 400, 500 or 600 animals) is removed annually over the next 10 years.